THE LATE PALEOCENE TO EARLY EOCENE POLAR FORESTS OF CANADA:

A PALEOBOTANICAL RECONSTRUCTION OF CLIMATE AND ECOSYSTEMS

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ABSTRACT

The Canadian High Arctic during the late Paleocene–early Eocene was home to an ecosystem composed of temperate and tropical flora and fauna. The fossil-bearing deposits on Ellesmere and Axel Heiberg islands contain the best of record of these, now extinct, high latitude ecosystems. These fossil flora are preserved in fluvial sediments indicative of a flood plain environment, with evidence of crevasse splay and deltaic deposits, interbedded with coal sequences, and rare layers of volcanic ash. The paleolatitude of these islands during the early Paleogene has been estimated at approximately ~75-80°N. These fossil floras have been placed stratigraphically in the upper Paleocene–lower Eocene, possibly occurring during or following one of the early Eocene hyperthermals (e.g. the Paleocene-Eocene Thermal Maximum or PETM, or the Eocene Thermal Maximum 2 or ETM2). Reported here is a comprehensive assessment of the character and composition of these now extinct high latitude forests.

Paleoclimate is assessed using physiognomic analysis of 3 leaf megafloras (Split Lake, Stenkul Fiord and Strathcona Fiord), and nearest living relative (Bioclimatic Analysis) on the palynoflora from the Margaret Formation from Ellesmere Island. Physiognomic approaches correlate modern leaf morphology with modern climatic parameters in order to reconstruct paleoclimate from fossil leaf assemblages. Nearest living relative methods estimate climate from fossil floras by association to modern floras and utilizing the climatic envelopes of the modern plants. The results of these analyses indicate high summer precipitation (228-249 cm/yr) and warm mean annual temperatures (10-12 °C) in the Arctic during the early Eocene, which in part corroborates prior floristic, faunal, and isotopic early Eocene Arctic studies.

Nevertheless, these results contradict a prior isotopic wood analysis that suggested seasonal precipitation or monsoonal conditions were a feature of these high latitude environments. Instead, present data are consistent with prior modeling studies that showed equable precipitation (i.e., precipitation distributed equally across the summer and winter

seasons) for these northern ecosystems. The equable precipitation regime, distributed across the summer light season and winter dark season, would have required a permanent to semi-permanent polar cloud cap, which may have contributed to regional warmth in the Arctic during the early Eocene.

In addition, a comprehensive morphotype catalogue of fossil plants is provided. This work utilizes multiple fossil localities from Ellesmere and Axel Heiberg islands, and forms a systematic framework that establishes an early Paleogene polar flora from High Arctic latitudes in Canada. A total of 62 ‘dicot’ angiosperm morphotypes, three monocotyledonous angiosperms, 13 gymnosperms, and five pteridophyte morphotypes are described and discussed in the context of the early Paleogene world. This work presents a significant contribution to the understanding of northern-polar biodiversity and environments during the warm greenhouse climate of the early Paleogene.

Finally, reported here are the first quantitative megafloral diversity estimates from Stenkul Fiord, Ellesmere Island, Canada, utilizing two purpose-made census-sampled collections supported by horizon-specific palynological analysis. Recent U-Pb geochronology places the fossil collections stratigraphically near the PETM and ETM2 hyperthermal events of the early Eocene. The fossil megafloras and palynofloras were analyzed using interpolation/extrapolation coverage-based rarefaction analysis using iNEXT in the R program, and compared against modern forests. Results of these analyses demonstrate that the early Eocene paleoarctic supported diverse forests ecosystems with floral diversity similar to modern mid-latitude broadleaf forests from North America, but that diversity was restricted as a result of photic seasonality. Furthermore, evidence shows that these ecosystems underwent floristic change probably related to the transient hyperthermal events.

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CA:	Coexistence Analysis
CAF:	Canadian Arctic Flora
CCA:	Canonical Correspondence Analysis
CLAMP:	Climate Leaf Analysis Multivariate Program
CMMT:	Cold Month Mean Temperature
EECO:	Early Eocene Climatic Optimum
ETM1:	Eocene Thermal Maximum 1
ETM2:	Eocene Thermal Maximum 2
GDGT:	Glycerol Dialkyl Glycerol Tetraether
GSP:	Growing Season Precipitation
LAA:	Leaf Area Analysis
LDG:	Latitudinal Diversity Gradient
LGS:	Length of Growing Season
LMA:	Leaf Margin Analysis
MAP:	Mean Annual Precipitation
MCR:	Mutual Climatic Range
MECO:	Middle Eocene Climatic Optimum
NALMA:	North American Land Mammal Ages
NLR:	Nearest Living Relative
NSERC:	National Science and Engineering Research Council
PETM:	Paleocene Eocene Thermal Maximum
SHRIMP:	Sensitive High-Resolution Ion Microprobe
US:	University of Saskatchewan
USPC:	University of Saskatchewan Paleobotany Collection
WMMT:	Warm Month Mean Temperature
WP:	Winter Precipitation
3WET:	3 Wettest Months precipitation
3DRY:	3 Driest Months precipitation

1. INTRODUCTION

The evolutionary path that has led to our modern plant biota is closely tied to the climatic history of our planet. As a result, fossil floral assemblages not only serve as a record of past climatic and environmental conditions, but also capture biotic trends of the distant past, evolutionary history, and biogeographic distribution (Manchester, 1999; Pigg and DeVore, 2010). Leaves, in particular, are plant organs that represent an interface between climate and phenotypic expression, insofar that the morphology of leaves will be influenced by climatic conditions. Foliar architectural adaptation to climatic and environmental stresses can be observed in the modern world. Thus, the relationship between climate and leaf architecture (e.g., margin, base, tip, shape) may be used to infer past climatic and environmental conditions from fossil leaves.

The late Paleocene and early Eocene is a notable time in Earth's history and is characterized by: a continental configuration that was similar to the present; the modernization of many plant and animal lineages, with many modern families established as integral parts of the vegetative landscape across North America; and, a warm equable greenhouse climate. The late Paleocene and early Eocene may be viewed as an experiment in deep-time, as this interval offers an opportunity to study biotic responses to a greenhouse climate punctuated by extreme warming events—an important analogue for our own warming climate.

Beginning in the mid-Paleocene, an approximate 10-million-year trend of global warming began that extended into the Eocene epoch (Kennett and Stott, 1991; Zachos et al., 2005; Lourens et al., 2005). The result was a geological interval of intense global warmth that peaked with the Early Eocene Climatic Optimum (EECO), the temperature acme for the whole of the Cenozoic (Zachos et al., 2001). This 10-million-year interval of warming was initiated by massive amounts of carbon being injected into the ocean and atmosphere (Zachos et al., 2011). The warming trend was periodically interrupted by several geologically short-lived transient

hyperthermal events (Kennett and Stott, 1991; Zachos et al., 2005; Lourens et al., 2005). These hyperthermal events (e.g. the PETM/ETM1, or Paleocene–Eocene Thermal Maximum/Eocene Thermal Maximum 1, and the ETM2, or Eocene Thermal Maximum 2) further perturbed the greenhouse climate of the early Eocene. The result was marked changes to climate at both the regional and global scale (Zachos et al., 2001, 2008).

Furthermore, during the early Eocene, the North American landscape underwent significant change. Extensive tectonism that began in the Paleocene and continued through the early Eocene started the renewed orogenic processes of the Rocky Mountain region (Graham, 1999). The northernmost part of the developing Rocky Mountain range experienced considerable volcanic activity from the early to late Eocene (Graham, 1999). The effects resulting from this prolonged interval of mountain building was to create a divide in between the vast intercontinental stretches of lowlands, effectively creating an eastern and western zone; and, the increased volcanic activity likely contributed to an additional rise in global temperatures (Wing, 1987; Graham, 1999).

Changes in climate and geography ultimately led to pronounced alteration of the evolution and distribution of vegetation in North America, such as the breakup of the relatively homogenous Paleocene North American vegetative province into distinct phytogeographic sub-regions, as well as the diversification of modern microthermal lineages (e.g. Rosaceae, Betulaceae, Sapindaceae) (Wing, 1987; Manchester, 1999).

The greenhouse conditions that prevailed during the late Paleocene and early Eocene allowed temperate trees and other thermophilic flora (e.g., palms and ferns) to extend into the polar latitudes, as well as increasing the range of many thermophilic fauna (Greenwood and Wing, 1995; Fricke and Wing, 2004; Sluijs et al., 2006, 2009; Eberle and Greenwood, 2012; Eldrett et al., 2014). Indeed, near the end of the early Eocene, plant lineages typical of tropical, subtropical, and warm-temperate vegetation had reached the greatest geographic extent they would ever achieve in the Cenozoic (Graham, 1999). Broad-leaf forests composed of tropical

and subtropical floral elements would continue to encroach poleward and ultimately dominate the mid-latitudes as global temperatures increased during the early Eocene (Wing, 1987; Manchester, 1999; Graham, 1999, 2011).

The Canadian High Arctic during the late Paleocene—early Eocene was home to an ecosystem composed of temperate and tropical flora and fauna. The fossil bearing deposits on Ellesmere and Axel Heiberg islands contain the best of record of these, now extinct, high latitude ecosystems (McIver and Basinger, 1999; Eberle and Greenwood, 2012). The climate, composition, and character of these high latitude forest ecosystems has long been the subject of both popular public and scientific inquiry (Heer, 1878; Basinger, 1986; McIver and Basinger, 1999). These forests were likely similar in biomass and primary production to modern old growth forests from the cool temperate regions of the Pacific northwest of North America (McIver and Basinger, 1999; Williams et al., 2009; Harrington et al., 2012). The climate of these early Paleogene polar regions in North America has been reconstructed to have been mild, equable, and temperate with winter temperatures remaining at or just above freezing (≥ 0°C) and warm summer temperatures (~20°C), estimates which result from a convergence of multiple proxies (Eberle and Greenwood, 2012 and references therein).

It has been postulated that the composition of these forests may have had an effect on regional climate and hydrology (Harrington et al., 2012). It is also likely that seasonal precipitation and temperature are connected, which may have had an influence not only on regional climate, but also global climate conditions during the early Eocene (Abbot et al., 2009; Shellito et al., 2009; Sluijs et al., 2009; Eberle and Greenwood, 2012; Eldrett et al., 2014). Climate parameters, primarily temperature or thermal seasonality, are recognized as a primary driver of the latitudinal diversity gradient (Archibald et al., 2010; Jardine et al., 2018; Brodie, 2019).

As the late Paleocene and early Eocene remain a focus for testing global climate models it is important to describe the character and composition of these ancient polar forests, as such this project had three primary goals:

1. Utilize paleobotanical evidence to reconstruct the paleoclimate of the early Eocene paleoarctic in Canada.
2. Develop a rigorous systematic framework for the late Paleocene-early Eocene fossil flora from Axel Heiberg and Ellesmere Islands, and describe each fossil floral element therein.
3. Explore the diversity of the paleoarctic forests from the Canadian High Arctic utilizing the paleobotanical fossil record.

The following chapters were written in manuscript style intended for publication; therefore, each chapter may be treated as a stand-alone document and has its own abstract, introduction, review of relevant literature, discussion of methods, conclusions, and references. In addition, these chapters were published as multi-author publications, and authorial contributions are listed and discussed below.

Chapter 2, "Was the Arctic Eocene 'rainforest' monsoonal? Estimates of seasonal precipitation from early Eocene megafloras from Ellesmere Island, Nunavut," is the first paper of this project (published as West et al., 2015) and quantifies the paleoclimatic parameters of the early Eocene paleoarctic in Canada. The study was conceived and conducted by me with the support of my supervisors Dr. David R. Greenwood, Dr. James F. Basinger. I organized the fossil morphotypes, performed the physiognomic climate analyses, and led the writing and interpretations, figure construction, and fossil photography. I oversaw the revision process and the writing of a rebuttal letter, with support from my supervisors, following two rounds of reviews.

Paleobotanical methods are utilized to reconstruct multiple climatic variables for the Canadian paleoarctic that use preliminary morphotypes established for the study. Estimates of temperature and precipitation were produced using univariate (Leaf Margin Analysis and Leaf Area Analysis) and multivariate (the Climate Leaf Analysis Multivariate Program) physiognomic analyses, as well as the nearest living relative method, Bioclimatic Analysis.

The local geology of three localities (i.e., Stenkul Fiord, Strathcona Fiord, and Split Lake) are discussed and the fossil floras are placed into stratigraphic context based on currently available relative and absolute dating information. Furthermore, the photic seasonality of these extinct polar environments is discussed, as well as the paleoclimatic, paleoecological, and paleoenvironmental implications of the resulting data. In addition to establishing both the geological and paleoclimatic context for the early Eocene fossil floras of the Canadian High Arctic, this paper gives some preliminary overview of the fossil flora, their historical significance, and their character; these subjects and ideas will be further expanded upon and discussed in greater detail in Chapter 3.

Chapter 3, "The late Paleocene to early Eocene Arctic megaflora of Ellesmere and Axel Heiberg islands, Nunavut, Canada," is a monographic treatment of the late Paleocene to early Eocene paleoarctic fossil flora from northernmost Canada (in press as West et al., 2019). I conceived and undertook this study under the supervision of Dr. James F. Basinger and Dr. David R. Greenwood. I created, refined, and described the fossil morphotypes upon which this study is based. I led the writing and interpretation, as well as figure construction and fossil photography, with contributions to editing and interpretation by my supervisors. Following the review process for this chapter, I took responsibility for revision as well as the writing of the rebuttal documents.

The historical identity and significance of this fossil flora and similar fossil floras from North America, Russia, Europe, and Greenland are discussed. Following this, the components of the fossil flora were sorted into informal taxonomic categories (i.e., morphotypes), and

described using methods detailed by Ellis et al. (2009, the Manual of Leaf Architecture), which allowed for the establishment of a systematic framework to be developed, dubbed the Canadian Arctic Flora. The strength of an informal taxonomic system is that it is unnecessary for morphotypes to be assigned to formal taxa for the fossil flora to be utilized for further paleoclimatic and paleoecological analyses.

Nevertheless, a rigorous literature review was undertaken and many of the morphotypes were assigned or compared to, previously established fossil plant taxa. Finally, the paleobiogeographic history of the fossil flora is briefly explored in the context of previously established paradigms for polar floras, and summaries of the similarities between the Canadian Arctic Flora and contemporaneous late Paleocene–early Eocene fossil plant sites from high- and mid-latitudes in North America, Russia, Europe, and Greenland.

The major contribution of this study is that it provides a significant addition to early Cenozoic paleobotany, and especially Arctic paleobotany. Although the fossil flora had been previously described in the late 1800's by the Swiss naturalist Oswald Heer (Heer, 1878), many of the determinations were inaccurate or incongruous with modern paleobotanical views. The fossil megaflora had since undergone limited taxonomic revision (McIver and Basinger, 1999), but a detailed analysis remained to be completed. Thus, this study presents the first contemporary detailed description, characterization, and analysis of the late Paleocene–early Eocene fossil flora from the Canadian High Arctic.

Chapter 4, "High Arctic forest diversity and floristic change during early Eocene hyperthermal events" explores the diversity of fossil sites from Stenkul Fiord on southern Ellesmere Island (submitted to *Science,* July 2019). I conceived the idea for this study and collected the fossils and sediment samples upon which the analyses and interpretations are based. I performed the data collection, diversity analyses, figure construction, and fossil photography. I led the writing and interpretation of this study. In order to build on the significance of my work, I collaborated with Mr. Markus Sudermann, who performed the pollen

identifications and data collection, an important contribution to this study, and this chapter will feature in his MSc. thesis as a result. Mr. Sudermann and Drs. Lutz Reinhardt (expedition leader for 2017 field work, and who provided stratigraphic control for my localities), Jennifer M. Galloway (co-supervisor for Markus Sudermann), David R. Greenwood (co-supervisors for both me and Markus Sudermann), and James F. Basinger also contributed to interpretation.

This study is composed of two major components. The first reconstructs diversity using purpose-made census-sampled leaf compression fossil collections from two stratigraphically disjunct sedimentary horizons anchored by absolute dating methods. The second expands on this concept and uses similarly well-constrained horizon-specific pollen analysis to further examine the diversity of these paleoarctic forests at both the local and regional scale.

These analyses revealed that the diversity of these high latitude forests was similar to the diversity of modern mid-latitude temperate deciduous broadleaf forests. Furthermore, these analyses were able to show that the diversity, essentially the number of morphotypes or taxa, of these forests remained relatively stable over time; however, the species composition in these forests did appear to change over time. The reason for these changes remains unresolved, although it is possible that these changes reflect depositional systems sampling different aspects of the forest at different times, rather than an external pressure resulting in species turnover. Potentially these changes may have occurred in response to the hyperthermal events ongoing throughout the early Eocene.

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2. WAS THE ARCTIC EOCENE 'RAINFOREST' MONSOONAL? ESTIMATES OF SEASONAL PRECIPITATION FROM EARLY EOCENE MEGAFLORAS FROM ELLESMERE ISLAND, NUNAVUT

This paper was published in the journal *Earth and Planetary Science Letters* and adheres to the style and format required by that journal, and appears as: WEST, C. K., GREENWOOD, D. R., & BASINGER, J. F. (2015): Was the Arctic Eocene 'rainforest'monsoonal? Estimates of seasonal precipitation from early Eocene megafloras from Ellesmere Island, Nunavut. *Earth and Planetary Science Letters*, *427*: 18-30.

Abstract: The early Eocene was the warmest interval of the Cenozoic, and included within it were several hyperthermal events, with the Paleocene–Eocene Thermal Maximum (PETM) the most pronounced of these. These globally warm climates extended into the Arctic and substantive paleobotanical evidence for high Arctic precipitation (MAP >150cm/yr) is indicative of an Arctic rainforest, which contradicts some climate models that show low Arctic precipitation. Prior studies of Arctic early Eocene wood stable-isotope chemistry, however, have shown a summer peak in precipitation, which suggests modern analogs are best sought on the summer-wet east coast of the Asia (e.g., China, Japan, South Korea), not the winter-wet west coasts of the Pacific Northwest of North America). Furthermore, some prior modeling data suggest that highly seasonal 'monsoon-type' summer-wet precipitation regimes (i.e., summer:MAP >55%) characterized certain mid and lower latitude regions in the early to mid-Eocene. Presented here is a new analysis using leaf physiognomy of 3 leaf megafloras (Split Lake, Stenkul Fiord and Strathcona Fiord) and palynofloral Bioclimatic Analysis from the Margaret Formation from Ellesmere Island, placed stratigraphically as early Eocene, possibly occurring during or following one of the early Eocene hyperthermals. These new data indicate high summer precipitation in the Arctic during the early Eocene, which in part corroborates the results from Eocene wood chemistry. Nevertheless, in contradiction to the wood analysis, monsoonal conditions are not indicated by our analysis, consistent with current modeling

studies. High summer (light season) and winter (dark season) precipitation in the Eocene Arctic during hyperthermals would have contributed to regional warmth.

Keywords: Arctic, Eocene, climate, paleobotany

2.1 INTRODUCTION

Global warming is currently causing Arctic temperatures to rise at two times the rate of lower latitudes, a trend that is predicted to continue affecting polar latitudes well into the future (ACIA, 2005; Serreze and Barry, 2011; Stroeve et al., 2012). The mild ice-free Arctic environments of the late Paleocene and early Eocene represent one of the best deep time analogs for evaluating a rapidly changing global climate on a high latitude system (Eberle and Greenwood, 2012). Some of the best examples of these ancient paleoenvironments can be found in the Canadian Arctic on Ellesmere Island (Fig. 2.1). This island and the surrounding region were once inhabited by lush swamp forests, and thermophilic fauna such as alligators and giant tortoises (Estes and Hutchison, 1980; McIver and Basinger, 1999; Eberle and Greenwood, 2012; Eberle et al., 2014).

The hyperthermals of the early Eocene are considered to be some of the most abrupt and dramatic climatic warming events of the entire Cenozoic (Zachos et al., 2008; McInerney and Wing, 2011). The rising warmth that began in the late Paleocene continued into the Eocene epoch (Zachos et al., 2008). The warming of the early Eocene led to two hyperthermal events, the PETM/ETM1 (Paleocene–Eocene Thermal Maximum, or Eocene Thermal Maximum 1) and the ETM2 (Eocene Thermal Maximum 2), as well as the prolonged warming of the EECO (Early Eocene Climatic Optimum) (Zachos et al., 2008). These hyperthermal events not only increased mean global temperatures, but also had an effect on hydrologic cycles (Pagani et al., 2006; Zachos et al., 2008; Leng et al., 2010; Hyland and Sheldon, 2013; Krishnan et al., 2014). The EECO resulted in a temperature acme not only for the Eocene, but for the entire Cenozoic

(Zachos et al., 2008). The PETM, however, represents the most abrupt and dramatic of these events, characterized by a negative carbon isotope excursion (between 2300 and 6800Gt ^{13}C depleted carbon; Ma et al., 2014) with temperatures rising 5–8 ºC in ≤ 20 ky with a global increase not exceeding 5 ºC, for 100–250 ky, making the PETM a useful analog for modern warming (e.g., Sluijs et al., 2006, 2007, 2009; Zachos et al., 2008; Dunkley-Jones et al., 2013; Wing and Currano, 2013; Eldrett et al., 2014).

Marked shifts in the character of precipitation characterized the PETM and the other Eocene hyperthermals, and the response on a regional scale was complex with shifts to wetter or drier climates recorded in different areas (Zachos et al., 2008). Mid-latitude environments that were warm and wet were marked by a decrease in precipitation that preceded or occurred during the PETM (Wing et al., 2005; Collinson et al., 2009; Garel et al., 2013; Kraus et al., 2013). High latitude environments that were temperate and wet, such as the Canadian High Arctic, Spitzbergen and North Sea, instead experienced an increase in both temperature and precipitation (Uhl et al., 2007; Greenwood et al., 2010; Eldrett et al., 2014). The north polar region of the early Paleogene represents an environment that has no satisfactory modern analogue, relegating it to fossil environment status, as defined in Jacques et al. (2014), although the winter-wet west coast forests of North America and the coastal forests of east Asia have been suggested as possible analogues (Greenwood et al., 2010; Schubert et al., 2012). Extensive studies in the literature document the presence of flora and fauna in the early Cenozoic that exist nowhere near these latitudes today (e.g., Hickey et al., 1983; Dawson et al., 1993; LePage and Basinger, 1991, 1995; McIver and Basinger, 1999; LePage, 2001, 2007; Lepage, 2003; Eberle, 2005; Eberle et al., 2014; Harrington et al., 2012). In addition, multiple studies have analyzed the climate of this fossil environment using paleontological and other available proxies from Arctic sediments (e.g., Greenwood and Wing, 1995; Jahren and Sternberg, 2003, 2008; Greenwood et al., 2010; Eldrett et al., 2009, 2014).

Although some climate models have shown low to moderate Arctic paleoprecipitation during the early to middle Paleogene (Shellito et al., 2003), the majority of studies have shown high precipitation (annual precipitation >150 cm/yr), mesothermal conditions (i.e., mean annual temperature ~12–15 ºC), and moderate winter temperatures (cold month mean temperature >0 ºC) characterized climates of high latitude Arctic rain forests during the late Paleocene through the PETM and into the middle Eocene (Greenwood et al., 2010; Eberle and Greenwood, 2012; Huber and Goldner, 2012). Notably, Huber and Goldner (2012) reconstructed global precipitation patterns of Eocene, identifying the existence of a robust global monsoonal precipitation pattern. In a summary of their model, much of the middle and lower latitudes of the Eocene were shown as monsoonal, while high latitudes such as the Arctic remained ever-wet or equable. However, Schubert et al. (2012) used a high-resolution carbon isotope analysis of fossil wood from the Arctic, showing a summer peak in precipitation that they defined as monsoonal.

Zhang and Wang (2008) noted that there are many different ways to define a monsoon and each definition can affect the interpretation of a monsoonal circulation. For the purpose of this study the definition and character of a summer monsoon follows the Zhang and Wang (2008) index for a region where the summer daily rate of precipitation is equal to 3 mm/day or more (i.e. 3 warmest months precipitation >28 cm), and the ratio of summer to annual precipitation exceeds 55% (Zhang and Wang, 2008). This index also accounts for the extended boreal winter and summer seasons, whereby summer is defined as May, June, July, August, September and winter is defined as November, December, January, February, March (Zhang and Wang, 2008).

Based on both paleoclimate proxy evidence and climate model sensitivity experiments, highly seasonal ‘monsoon-type’ summer-wet precipitation regimes seem to have characterized the early Eocene hyperthermal conditions in several regions of the earth (e.g., Greenwood, 1996; Hubert and Goldner, 2012), as well as the Arctic and Antarctic (e.g., Huber and Goldner,

2012; Schubert et al., 2012; Jacques et al., 2014; Krishnan et al., 2014). However, other proxy and modeling data for Arctic regions implies Eocene polar rain forests consistent with no or low precipitation seasonality (Eldrett et al., 2009; Greenwood et al., 2010; Eberle and Greenwood, 2012; Huber and Goldner, 2012). The hydrological cycle of a post-PETM high latitude environment, as evidenced by climate models and paleo-precipitation reconstructions from paleobotanical proxy data, was likely a significant component in maintaining high-latitude warm and equable climates (Abbot et al., 2009; Heinemann et al., 2009; Greenwood et al., 2010; Speelman et al., 2010; Tindall et al., 2010; Huber and Caballero, 2011; Huber and Goldner, 2012; Pross et al., 2012; Schubert et al., 2012; Kiehl and Shields, 2013).

Presented here is a new analysis applying Leaf Area Analysis (LAA), Leaf Margin Analysis (LMA) and Climate Leaf Analysis Multivariate Program (CLAMP) to 3 leaf megafloras from 3 separate localities within the Margaret and Mount Moore Formations (Split Lake, Stenkul Fiord, and Strathcona Fiord), as well as a palynoflora from Stenkul Fiord, all from Ellesmere Island (Fig. 2.1). These floras can be stratigraphically placed as latest Paleocene or early Eocene in age (Kalkreuth et al., 1996; Harrison et al., 1999; Eberle and Greenwood, 2012; Harrington et al., 2012; Schubert et al., 2012; Reinhardt et al., 2013), and therefore present an opportunity to evaluate regional precipitation at high northern polar latitudes during the globally warm early Paleogene.

2.2 **GEOLOGICAL CONTEXT**

The early Paleogene fossil localities on Ellesmere Island and Axel Heiberg islands are part of a series of units that constitute the Eureka Sound Group. The formations which encompass the Eureka Sound Group span the Late Cretaceous to the middle Eocene in age (Miall, 1986; Ricketts, 1986, 1994; Harrison et al., 1999; Thorsteinsson et al., 2009; Eberle and Greenwood, 2012; Reinhardt et al., 2013).

Miall (1986) divided the Eureka Sound Group into 7 formations on the basis of research on central and southern Ellesmere, with the Mount Bell and Vesle Fiord Formations most basal and equivalent in age. Stratigraphically above these formations were the Mount Lawson, Mount Moore, and Margaret Formations (Miall, 1986). Ricketts (1986), however, divided the Eureka Sound Group into 4 formations based principally on his work on Axel Heiberg and northern Ellesmere: the Expedition, Strand Bay, Iceberg Bay, and Buchanan Lake Formations. The fossils used in this study are from the Margaret and the Mount Moore Formations of Miall (1986). The Margaret Formation at Stenkul Fiord is considered correlative with the Iceberg Bay Formation of Ricketts (1986), whereas the Mount Moore Formation is correlative with the Iceberg Bay and upper-most Strand Bay Formations of Ricketts (1986) (Harrison et al., 1999; Eberle and Greenwood, 2012) (Fig. 2.2).

Lithologically, the Margaret (Iceberg Bay) Formation consists of coarsening-upward cycles of interbedded cross-bedded sand, silt, and mudstone packages that also feature coals. The depositional environments of these sedimentary packages have been interpreted as a proximal delta-front to delta-plain environment with abundant channels and coal swamps (Miall, 1986; Ricketts, 1986). The Mount Moore Formation consists of shallow marine sandstones, which range from fine to very fine with a predominance of small-scale ripple marks, which are indicative of a low energy environment (Miall, 1986). The depositional environment was described by Miall (1986) as enigmatic and that no existing facies model was suitable for comparison, with a protected marine embayment or estuary as the most likely depositional environment.

2.2.1 **STRATIGRAPHY**

The fossil megaflora from Strathcona Fiord and Split Lake were sampled from the Mount Moore Formation, which was assigned an age of late Paleocene to early Eocene by Miall (1986). The Mount Moore Formation at Split Lake was dated from zircon crystals found in an

ash bed in the Mount Lawson Formation which conformably underlies the Mount Moore Formation; sensitive high-resolution ion microprobe (SHRIMP) analysis yielded a U–Pb age of 53.9 ± 3.1 Ma, which provides an age of latest Paleocene to early Eocene (Miall, 1986; Reinhardt et al., 2013). Paleomagnetic analyses of the Mount Moore Formation at Strathcona Fiord are consistent with deposition occurring during Chron C26–25 which is late Paleocene in age (Tauxe and Clark, 1987). Bivalves and gastropods found in this formation are also indicative of a late Paleocene age (Marincovich and Zinsmeister, 1991).

The fossil megaflora from Stenkul Fiord was sampled from strata which were assigned to the Margaret Formation by Miall (1986). The coal, sandstone and siltstone strata of Stenkul Fiord, as well as other correlative members of the Margaret Formation, have been dated palynologically as late Paleocene to early Eocene (Kalkreuth et al., 1993, 1996; Harrison et al., 1999). Vertebrate fossils have been found at two stratigraphic levels of the Margaret Formation near Bay Fiord on central Ellesmere Island (Dawson, 1990, 2001; Eberle and McKenna, 2002), and include fossil taxa that are indicative of the early Eocene Wasatchian and early–middle Eocene Bridgerian North American Land Mammal Ages (NALMA), respectively (Dawson et al., 1993; West et al., 1981; Eberle and Greenwood, 2012; Eberle and Eberth, 2015). Vertebrate fauna from the Margaret Formation of the southern shore of Stenkul Fiord, however, indicate these strata are from the early Wasatchian (Graybullian, 53.0–54.5 Ma) NALMA (Eberle and Greenwood, 2012; Harrington et al., 2012; Eberle and Eberth, 2015).

Zircon crystals recovered from volcanic ash from coal, sand and siltstone cropping out of Margaret Formation on the southern shore of Stenkul Fiord were dated using SHRIMP analysis and yielded a U–Pb age of 52.6 ± 1.9 Ma, indicating an early Eocene age (Reinhardt et al., 2013), although due to the small number of zircon grains recovered the authors caution that this age is considered preliminary. The age of the volcanic ash (52.6 ±1.9), and the Graybullian NALMA correlation of the vertebrate fauna from Stenkul Fiord, provide a time range that predates the EECO and potentially captures the ETM2 (Fig. 2.2) (Eberle and Greenwood, 2012;

Eberle and Eberth, 2015). The fossil megafloras sampled from Stenkul Fiord are thus early Eocene in age, and are representative of flora from after the Paleocene–Eocene boundary but before the EECO (Fig. 2.2) (Harrington et al., 2012). Pollen was sampled by Harrington et al. (2012) from two sections at Stenkul Fiord, labeled as M and P (Fig. 2.1). The two sections overlap and were sampled across a visible white sand marker bed (Harrington et al., 2012), while the megafloras were recovered from below the white sand marker bed. The Wasatchian Stenkul Fiord vertebrate fauna noted above included a fossil turtle belonging to the family Emydidae recovered from the white sand marker bed, and the perissodactyl *Homogalax* higher in the section (Holroyd et al., 2001; Harrington et al., 2012; Eberle and Eberth, 2015).

2.3 **MATERIALS**

The extensive fossil megaflora (i.e., leaves, shoots, and other plant organs) collections used for this analysis are mostly from overbank and lacustrine shale faces. These fossils are housed within the University of Saskatchewan Paleobotanical Collection (USPC), which includes a diversity of localities found between 77 ºN and 82 ºN on Ellesmere Island and Axel Heiberg islands (part of the Canadian Arctic Archipelago), northern Nunavut (Fig.1). The megafloras examined for this analysis were collected on Ellesmere Island from Strathcona Fiord (US422), Stenkul Fiord (US435–436 & 438–439), and Split Lake (US442 & 444) (Fig. 2.1).

These three sites are each characterized by a mix of large-leafed and small-leafed dicot taxa (Figs. 2.3, 2.4, 2.5), with overall mean leaf size across all leaf morphotypes comparable to that previously reported for late Paleocene to middle Eocene floras from Ellesmere and Axel Heiberg islands (McIver and Basinger, 1999; Greenwood et al., 2010). Bioclimatic Analysis is used here to evaluate the Stenkul Fiord palynoflora from Harrington et al. (2012). Based on current stratigraphic understanding, the fossil flora sites included in this study are from the late Paleocene and early Eocene, may include the PETM and ETM2, and so offer insights into

Arctic climate during the warmest parts of the early Eocene (McIver and Basinger, 1999; Harrison et al., 1999; Eberle and Greenwood, 2012; Harrington et al., 2012).

Prior climatic analysis of similar floras has focused on late Paleocene and middle Eocene floras (e.g., Greenwood et al., 2010), principally the middle Eocene climatic optimum or 'MECO'. The Stenkul Fiord site has received particular attention for its numerous fossil beds, with studies featuring both plants (e.g. Hickey et al., 1983; McIver and Basinger, 1999; Williams et al., 2009), and animals (e.g. Estes and Hutchison, 1980; Dawson, 1990; Eberle and McKenna, 2002; Eberle and Eberth, 2015). The Stenkul Fiord locality also was the focus of the recent studies that identified a monsoonal climate for early Eocene Arctic environments as well as details on plant diversity in the Eocene Arctic forests (Harrington et al., 2012; Schubert et al., 2012). Here we apply a range of leaf physiognomic methods, as each approach has limitations. By including estimates from the different methods and calibration sets (e.g., CLAMP, Leaf Area Analysis and Leaf Margin Analysis), we expect that our compilation results are more useful for interpretation of Arctic early Eocene climates.

2.4 **METHODS**

2.4.1 **CLAMP**

The Climate Leaf Analysis Multivariate Program (CLAMP) developed by Wolfe (1993) is a multivariate system utilizing a compilation of modern vegetation data and their associated climate data from major regions around the globe. The calibration of numerical relationships between leaf architecture and climate parameters of modern vegetation allows for the determination of ancient climatic data from fossil assemblages. CLAMP is used in conjunction with canonical correspondence analysis (CCA), a direct ordination method which mathematically assigns climate vector relationships (Kovach and Spicer, 1996; Spicer, 2000).

The database used in CLAMP applies 31 different leaf characters to produce 11 different climate parameters (Spicer, 2000). Leaves are scored and then compared against a number of

modern climate databases, and vectors for each of the climate variables being tested for can be calibrated (Teodoridis et al., 2011). Fossil leaves are scored in the same manner as the modern vegetation calibration data set, and paleoclimate variables are derived from modern vegetation–climate databases (Spicer, 2000). The CLAMP Physg3brcAZ+GRIDMET3brcAZ datasets consisting of 144 different modern vegetation sites (Yang et al., 2011) were used to perform the CLAMP analysis.

It is recommended that to adequately reconstruct climate using CLAMP a fossil sample should contain at least 20 species (or leaf morphotypes), with a preference for sample sets that exceed 30 species in order to minimize uncertainty (Wolfe, 1993; Spicer et al., 2005; Teodoridis et al., 2011; Yang et al., 2011). Samples with fewer than 20 morphotypes will have larger uncertainties than the reported analytical errors, and results from these analyses should be considered preliminary. Due to the limitations of field collections, fewer than 20 morphotypes were available for Strathcona Fiord and Split Lake; however, the Stenkul Fiord collection exceeded the recommended morphotype minimum (Table 2.1). The method used to perform a CLAMP analysis for paleoclimatic reconstruction followed the CLAMP procedure outlined on the CLAMP website (http:/ /clamp.ibcas.ac.cn).

2.4.2 **LEAF AREA ANALYSIS**

Leaf size has shown a strong correlation to water supply, i.e., plants in wet climates have large leaves and those in dry climates have small leaves, as venation density scales with leaf size and small leaves with high vein density show the greatest drought tolerance (Wilf et al., 1998; Peppe et al., 2011; Scoffoni et al., 2011), and thus leaf area has been used as a proxy for mean annual precipitation (MAP). Despite large standard errors, Wilf et al. (1998) were able to demonstrate that the mean leaf area of a locality acts as a proxy for MAP. Peppe et al. (2011) produced an alternative method for calculating MAP from megafloras; however, their method had poor regression statistics and had much larger standard errors than the original calibration of Wilf et

al. (1998), owing to the inclusion of modern vegetation sites from non-tropical broadleaf evergreen as well as broadleaf deciduous vegetation. In addition, the digital physiognomic precipitation calibration of Peppe et al. (2011) was not used, as many of the specimens are fragmentary, in some cases ≤25% preservation, and would not be able to be applied to the entire flora. The leaf area analysis direct measurement approach of Wilf et al. (1998) was applied (1), where leaf area is measured and averaged for the smallest and largest specimens for each dicot morphotype and converted to a natural log (MlnA). The global equation of Peppe et al. (2011) was also applied (2). The standard error for each equation is converted from natural log values (ln) and is therefore asymmetric (Wilf et al., 1998; Peppe et al., 2011).

$$\ln(\mathrm{MAP}) = 0.548 \cdot \mathrm{M\ln A} + 0.768 \quad (1)$$

$$\ln(\mathrm{MAP}) = 0.283 \cdot \mathrm{M\ln A} + 2.92 \quad (2)$$

2.4.3 **LEAF MARGIN ANALYSIS**

The architecture of a leaf margin, either toothed or untoothed, has a strong correlation to mean annual temperature (MAT) (Bailey and Sinnott, 1916; Wolfe, 1979; Wilf, 1997; Kowalski and Dilcher, 2003; Peppe et al., 2011). MAT is calculated from the proportion of untoothed leaves in a flora. The Leaf Margin Analysis (LMA) regression equations used here are the classic LMA equation (3) from Wolfe (1979) and Wing and Greenwood (1993). As a number of studies have shown that the correlation between the proportion of untoothed leaves in a flora and the MAT show regional variations world-wide (Gregory-Wodzicki, 2000; Greenwood et al., 2004; Spicer et al., 2004; Royer et al., 2012), the global LMA equation (4) from Peppe et al. (2011) was also applied. Standard error for classic LMA is calculated from the number of morphotypes in a flora as per the Wilf (1997) equation (5) where *r* is the number of morphotypes. Standard error for the global LMA equation was calculated by Peppe et al. (2011) and is 4.8 ºC. Similarly to LAA, the digital physiognomic temperature calibration of Peppe et al. (2011) was not applied to the

Ellesmere Island flora as many of the specimens are fragmentary, in some cases ≤25% preservation, and the method would not be able to be applied to the entire flora.

$$MAT = 30.6P + 1.14 \quad (3)$$

$$MAT = 20.4P + 4.60 \quad (4)$$

$$\sigma MAT = 30.6 \sqrt{(1 - P)/r} \quad (5)$$

2.4.4 **MORPHOTYPES**

One of the strengths of physiognomic approaches is that taxonomic identifications are unnecessary for an analysis; however, grouping the fossil leaves into distinct categories called morphotypes is necessary to adequately compare and score the flora against modern datasets (Spicer, 2000; Teodoridis et al., 2011; Yang et al., 2011). These morphotypes are often considered parataxonomic in their construction, and generally emulate the species concept without the need for taxonomic assessment (Ellis et al., 2009). All dicot leaf specimens from each locality were assigned to morphotypes and scored for physiognomic analysis. Details of the sites' leaf morphotypes, CLAMP score data, leaf area, and leaf margin proportion values are provided in the online supplementary materials.

2.4.5 **NEAREST LIVING RELATIVE ANALYSIS**

The climatic tolerances of a fossil's nearest living relative can be applied to fossil assemblages, and an overlap of climatic tolerances can be produced which forms the "coexistence interval" or 'Mutual Climate Range', an interval which can be determined for any climatic parameter (e.g., Hickey et al., 1988; Mosbrugger and Utescher, 1997; Thompson et al., 1999, 2012; Eldrett et al., 2014).

Bioclimatic Analysis (Greenwood et al., 2005, 2010) is essentially equivalent to Mosbrugger and Utescher's (1997) Coexistence Analysis (CA), and relies upon similar methods

of climate reconstruction. The difference between these two methods results from how outliers are dealt with, i.e. those taxa that exist outside the zone of overlap created from the majority of taxa used in the reconstruction. In CA, outliers are simply removed before the coexistence intervals are determined, whereas in Bioclimatic Analysis (sensu Greenwood et al., 2005; Pross et al., 2012; Eldrett et al., 2014) climate is estimated using the 10^{th} (lower limit) and 90^{th} (upper limit) percentile of the total range for taxa used in the analysis. This statistical process objectively removes extreme outliers, consistent with recent recommendations (Grimm and Denk, 2012; Thompson et al., 2012; Eldrett et al., 2014).

Similar to Bioclimatic Analysis is the Mutual Climate Range (MCR) approach, which is developed from the 0^{th} and 100^{th} percentiles of the taxa used (Thompson et al., 2012). Bioclimatic analysis and MCR have both been used previously, with results matching other independent proxies such as stable isotopes for reconstruction of Cenozoic paleoclimates (Greenwood et al., 2010; Eldrett et al., 2009, 2014; Thompson et al., 2012; Kotthoff et al., 2014). For this study, the majority of climate profiles for NLRs were obtained from Thompson et al. (1999, 2012) and Fang et al. (2011) for trees and shrubs, and the online database of Natural Resources Natural Resources Canada (2012) for non-trees, supplemented by data from sources outlined in Eldrett et al. (2014) and Kotthoff et al. (2014).

2.5 **RESULTS**

2.5.1 **TEMPERATURE RECONSTRUCTION**

The estimates of MAT from CLAMP (Table 1) for the three Ellesmere Island localities produce a range of 10.6–16.5 ºC, while the MAT estimates from LMA (Table 2) range from 6 to 16 ºC from the classic LMA equation (Wing and Greenwood, 1993), and range from 5 to 17 ˚C from the Peppe et al. (2011) global LMA equation. While the estimates from CLAMP for two of the sites had fewer morphotypes scored than the recommended 30, our estimates are similar to previous estimates of 8–15 ºC for early to middle Eocene climate reconstructions for this region

using Eocene arctic fossil flora (Basinger et al., 1994; Greenwood and Wing, 1995; Greenwood et al., 2010; Eberle and Greenwood, 2012), as well as isotopic proxies from middle Eocene floras of the Buchanan Lake Formation of Axel Heiberg Island (Jahren and Sternberg, 2003; Eberle et al., 2010). The warm month mean temperature (WMMT) estimate derived from CLAMP produced a range of 19.5–27 ºC, and the cold month mean temperature (CMMT), 0–8 ˚C.

These temperature ranges (Table 2.1) are consistent with previous temperature reconstructions which have suggested summer temperatures >20 ºC and winter temperatures >0 ºC (Greenwood et al., 2010; Eberle et al., 2010). The MAT and CMMT of the Ellesmere Island localities are similar to modern west-coast rain forests of British Columbia (e.g., Tofino, MAT 9.5 ºC and CMMT 4.5 ºC; Environment Canada, 2014), as well as east-coast localities of Southeast Asia (e.g., Gangneung, Korea, MAT 13.1 ºC and CMMT 4.1 ºC; Korea Meteorological Administration, 2015; and Chōshi, Japan, MAT 15 ºC and CMMT 8.5 ºC; Japan Meteorological Agency, 2015). MAT estimates (Table 2.2) derived from the palynoflora lists from Harrington et al. (2012) using Bioclimatic Analysis produced a MAT temperature range of 8–20 ºC with an average temperature of 15.4 ºC across both sections (M & P), a range supported from both paleofloral and isotope proxies, and analysis of glycerol dialkyl glycerol tetraether (GDGT) membrane lipids of soil bacteria (Basinger et al., 1994; Weijers et al., 2007; Eberle et al., 2010).

The Bioclimatic Analysis produced estimates of WMMT and CMMT that range from 17 to 27 ºC and from −3.0 to 13 ºC, respectively. The CMMT range suggests a possible minimum winter temperature slightly cooler than has been previously estimated (Greenwood and Wing, 1995). There is no significant change in temperature between the two stratigraphic sections (M & P), nor is there a significant difference between the estimates from above and below the Stenkul Fiord white sand marker bed. The equable annual temperatures produced by these analyses would have been sufficient to support the presence of the thermophilic terrestrial biota

that have been found in the region, including hippo-like *Coryphodon*, tapirs, primates, giant tortoises, alligators, snakes, and temperate fish (e.g., Eberle and Greenwood, 2012; Eberle et al., 2014).

2.5.2 **PRECIPITATION RECONSTRUCTION**

The MAP estimates from LAA (228–240 cm/yr with an error range of −69/+104 from LAA using Wilf et al., 1998; 206–211 cm/yr with an error range of −94/+178 from the Peppe et al., 2011 global LAA; Table 2.2) are similar to, but higher than precipitation estimates derived by LAA from megafloras of the late Paleocene Lower Coal Member of the Iceberg Bay Formation (153 cm/yr −46/+66 cm) and middle Eocene Buchanan Lake Formation (133 cm/yr with an error range of −40/+57 cm) (Greenwood et al., 2010). The Ellesmere Island Eocene sites show MAP generally consistent with modern temperate rainforest ecosystems in British Columbia, and at times exceeding even the wettest rain forests of these areas when the upper boundary of the error range is considered for MAP (e.g., Tofino, BC, 326 cm/yr, 3-wet months 137 cm, 3-dry months 30 cm; Environment Canada, 2014), and exceeds precipitation values for east-coast localities of Southeast Asia (e.g., Gangneung, Korea, 146 cm/yr, 3-wet months 78.5 cm, 3-dry months 14 cm; Korea Meteorological Administration, 2015; and Chōshi, Japan, 156 cm/yr, 3-wet months 55 cm, 3-dry months 25 cm; Japan Meteorological Agency, 2015).

The MAP results from Bioclimatic Analysis (115–125 cm/yr with an error range of 33–41 cm; Table 2.3) produced results similar to, but lower than the late Paleocene Lower Coal Member of the Iceberg Bay Formation and middle Eocene Buchanan Lake Formation (Greenwood et al., 2010), and these results were also significantly lower than the LAA MAP results. Estimates from BA are produced from the overlapping climatic ranges for all taxa within a sample. These ranges represent an envelope of conditions required to support each taxa. This must be considered when interpreting the results, as certain taxa may require very specific conditions which are not representative of the entire site vegetation. It is also important to note

that pollen samples from a given location may ultimately be derived from a much larger area, and this may also alter the climate estimate as the influence of local climate conditions is reduced. The results from these two analyses, however, do overlap at the lower margin of the LAA and the upper margin of the BA. The values produced by Bioclimatic Analysis may be the result of the pollen samples occurring above the megaflora in the sediment column, and might represent a change in regional climate. There is no significant amount of change in precipitation between the two stratigraphic sections (M & P), nor is there a significant difference between the estimates from above and below the white sand marker bed.

2.6 **PRECIPITATION SEASONALITY**

Recent studies of modern monsoonal sites have shown that leaf physiognomy can be used in identification of summer-precipitation-dominated monsoonal climates (Jacques et al., 2011, 2014). This same signal would also be present in ecosystems that would become dormant during the long dark winters of high latitude regions (Royer et al., 2003; Jahren and Sternberg, 2008). LAA estimates of MAP may be biased towards precipitation during the Arctic summer, as a result of the winter dormancy. The Arctic summer would have spanned 6–8 months in duration (Table 2.1). Regions that exhibit monsoons, or "monsoon-type" summer-wet precipitation (i.e., summer:MAP >55%; Zhang and Wang, 2008) are not seasonally equable.

These types of monsoonal precipitation regimes have been proposed using both proxies and modeling data to characterize Eocene hyperthermal conditions in several regions of the earth, including the Arctic and Antarctic (Huber and Goldner, 2012; Schubert et al., 2012; Jacques et al., 2014). However, in polar regions proposed summer-wet precipitation regimes are contradicted by other proxy evidence (Greenwood, 1996; Eberle and Greenwood, 2012). The results from this study also contradict the monsoonal model, and rather are consistent with the modeling studies of Huber and Goldner (2012), that show Ellesmere Island and the surrounding region of the Arctic as 'ever-wet'.

Schubert et al. (2012) applied isotopic analyses to fossilized wood from the High Arctic, using $\delta^{13}C$ to produce models that showed a high degree of seasonal precipitation: approximately 75% of the MAP falling during the summer polar light season. The dark polar winter as a result would have been comparatively dry. This degree of seasonality, where the ratio of summer precipitation to MAP is greater than 55% (Zhang and Wang, 2008), implies a summer monsoonal precipitation regime for the early Eocene Arctic. Nevertheless, LAA analyses of the 3 Arctic megaflora have produced MAP estimates which far exceed the growing season precipitation (GSP) estimates produced by the CLAMP analyses (Table 2.1).

The growing season would have occurred during the polar light season (LGS 6–8 months); therefore, GSP probably approximates summer precipitation. The difference between MAP and GSP (6) may be used to approximate winter precipitation, even though the LAA MAP estimates may be biased towards summer precipitation.

$$WP = MAP - GSP \quad (6)$$

The result from equation (6) is a range for winter precipitation (WP) (Table 2.4) which nearly equals or exceeds that of summer precipitation (GSP). The LAA results from using the global equation of Peppe et al. (2011) produces a much larger range, a result indicative of the higher error values attributed to this equation. The CLAMP estimates for the 3 wettest months precipitation (3WET) and the 3 driest months precipitation (3DRY) differ by 17–50% (Table 2.1), indicating some seasonality of precipitation, although it remains impossible to state which of 3WET and 3DRY represents summer. Spicer et al. (2009) noted that these values should only be regarded as an indicator of the degree of seasonal variation in precipitation and not as winter vs. summer seasonality. Additionally, it has been noted that the 3WET value is generally wetter than the observed values of the vegetation training sets (Spicer et al., 2011). Although a difference between 3WET and 3DRY (Table 2.1) is seen, this difference may not be as

considerable, as the 3WET value may be overestimated. Though some seasonal variation was likely, it can thus be concluded that the polar winter was probably not as dry as has been previously suggested by Schubert et al. (2012), i.e. even the driest season experienced significant precipitation (3DRY 26.5–31.3 cm, Table 2.1). This is consistent with previous Eocene climate modeling by Huber and Goldner (2012). The existence of a wet winter corroborates earlier hypotheses that a possible modern analog for the forests of the High Arctic closely resembled the winter-wet rainforests of the North American west coast (Greenwood et al., 2010), rather than the summer-wet rain-forests of the Asian east coast, which show a marked winter dry season.

2.7 **PHOTIC SEASONALITY**

Similarly to the modern day, the High Arctic during the early Paleogene experienced lengthy periods of continuous light and dark during the respective polar summer and winter. The extremity of the photoperiod constituted a form of photic seasonality. The lush forests of the Arctic are well known for their deciduous habit, which included not only angiosperms, but also gymnosperms (e.g., dawn redwood, cypress, larch, golden larch). It has been proposed that deciduousness may have served as a means to limit carbon loss throughout the polar night (Wolfe, 1980; Axelrod, 1984) and that thereby a means to survive the polar winters by entering a period of dormancy (Basinger et al., 1994). Experimental evidence, however, has suggested that limitation on carbon loss may not have been the driving factor in explaining the dominance of the deciduous habit at high latitudes (Osborne and Beerling, 2003; Osborne et al., 2004; Royer et al., 2003, 2005).

Although we are unsure why the deciduous habit dominated the lush Arctic forests of the early Paleogene, there is agreement that the abscission of leaves combined with 4–8 months of continuous twilight and darkness would have caused the flora to become dormant (e.g., Wolfe, 1980; Francis, 1990; Basinger et al., 1994; Royer et al., 2003; Spicer et al., 2004; DeVore and

Pigg, 2013). It is unclear, however, if the broad-leaf deciduous angiosperms of the Arctic became fully dormant as their modern temperate counterparts do, or if they instead enter one or two of the three stages of dormancy (i.e., paradormancy, endodormancy, and ecodormancy; Horvath et al., 2003). DeVore and Pigg (2013) suggested that due to the warmth of the Eocene Arctic that true dormancy may not have been achieved, and the cold-resistant nature of our temperate zone trees evolved much later.

Plants possess the genetic capacity to adapt to their complete growing season, not simply the conditions prevailing during leaf development (Spicer et al., 2004). Since deciduous trees drop their leaves when entering dormancy, it could be argued that no selective pressures would act upon leaf architecture to indicate winter or polar night conditions (Spicer et al., 2004). This, however, is not the case, as Spicer et al. (2004) were able to show that the vegetation data sets used for CLAMP are able to code for temperatures below zero, even though many of the taxa are deciduous. Thus CLAMP studies have shown that climate variables are still captured during periods of dormancy (e.g. CMMT and MAT), or are at least reflective of the rate of spring warming (Spicer et al., 2004). As the leaves are responding to spring warming, it is expected that they are coding in their architecture the availability of water during emergence from dormancy; in short, the leaves would reflect the period that would precede the warming responsible for wind reversals that facilitate a summer monsoonal precipitation regime.

It is important to note that despite 24 h of sunlight during the polar summer, the light at high latitudes is primarily low angle with decreased photosynthetically available radiation and lower wavelengths more effectively scattered (Taulavuoriet al., 2010). In addition, the enhanced hydrological cycle of the Eocene Arctic would have promoted cloud generation and may have resulted in a permanent cloud cap that would have further diffused incoming solar radiation (Herman, 1994; Abbot et al., 2009; Kiehl and Shields, 2013). The diffuse high latitude light may have favored the production of larger leaves, just as shade leaves are larger than sun leaves (Lichtenthaler et al., 1981).

Despite dormancy during the polar winter, and a tendency towards larger leaves during the polar summer, the Arctic flora would still capture a snapshot of regional high latitude early Paleogene climate; however, a degree of uncertainty is still inherent and could produce a summer bias in the results. An Arctic 'summer bias' is reported for biogeochemical temperature proxies (Eberle et al., 2010).

2.8 **PALEOCLIMATIC, PALEOECOLOGICAL, AND PALEOENVIRONMENTAL IMPLICATIONS**

A climate model that includes dry winters coupled with lengthy periods of continual darkness presents a challenge when trying to explain frost-free winters at high latitudes. Wet winters, however, would have had a pronounced effect on atmospheric latent heat flux, and high levels of humidity (~80%, Table 1) would have improved atmospheric insulation (Abbot et al., 2009; Kiehl and Shields, 2013). Climate simulations have suggested that increasing global temperature would have increased global precipitation, by as much 2 to 3% for every ºC increase (Held and Soden, 2006). This may have had a more severe effect at the poles, and may have perpetuated a positive feed-back loop of warm temperatures and high annual precipitation.

Close proximity to a warm Arctic Ocean would have led to atmospheric interaction and may have also influenced Arctic temperatures, a mechanism that has been previously evoked as a means to sustain the polar forests that were common in the Late Cretaceous (Shellito et al., 2009; Spicer and Herman, 2010; Kiehl and Shields, 2013). The warm MAT and the above-freezing winter temperatures (Tables 2.1 and 2.2) were able to support a rich thermophilic terrestrial fauna including hippo-like *Coryphodon*, tapirs, primates, giant tortoises, alligators, snakes, and temper-ate fish (e.g., Eberle and Greenwood, 2012; Eberle et al., 2014; Eberle and Eberth, 2015). The warm winter temperatures influenced by an active winter hydrologic system may have allowed *Coryphodon*, other large mammals (e.g. tapirs and other perissodactyls), and reptiles to remain resident in the Arctic during the long polar night (Eberle et al., 2009).

The high MAP and relative humidity estimates from our study (Tables 2.1 and 2.2) are consistent with an early Paleogene environment supporting polar rain forests, with evidence of a very active hydrological cycle in effect as far back at the Late Cretaceous at high latitudes (Spicer and Herman, 2010 and references therein). These estimates are also consistent with climate for the Eocene modeled by for example Greenwood et al. (2010) and Huber and Goldner (2012). The enhanced Arctic hydrological cycle coupled with greenhouse conditions would have resulted in precipitation exceeding evaporation, which would have caused significant continental runoff into the nearby Arctic Ocean (Pagani et al., 2006).

The amount of precipitation and high humidity would have supported a landscape dominated by inland swamps, and coastal wetlands (McIver and Basinger, 1999; Barke et al., 2012). This is consistent with sedimentological evidence, such as abundant coal seams and the absence of red beds (Miall, 1986). Studies of late Paleocene sediments in the ACEX core from Lomonosov Ridge have shown the presence of inertinite and pyrofusinite, indicators that wild fires were occurring during deposition (Boucsein and Stein, 2009). Early Eocene sediments analyzed higher up in the core have negligible inertinite or other fire indicators (Boucsein and Stein, 2009). This decrease or absence of inland fires may have resulted from an increase in precipitation due to the onset of the hyperthermals. These wet conditions may have contributed to the freshening of the Arctic Ocean, an ocean which periodically supported brackish species of shark and blooms of the fresh water fern *Azolla* (Brinkhuis et al., 2006; Kim et al., 2014).

2.9 **CONCLUSIONS**

Using three megafloras from Ellesmere Island, Canada, estimates of temperature, precipitation and other climate variable were produced using physiognomic methods (i.e., Leaf Area Analysis, Leaf Margin Analysis, and Climate Leaf Analysis Multivariate Program), as well as a nearest living relative method (i.e., Bioclimatic Analysis). The temperature estimates are in agreement with previous proxy evidence, both isotopic and paleobotanical (Basinger et al.,

1994; Greenwood and Wing, 1995; Jahren and Sternberg, 2003; Eberle et al., 2010; Greenwood et al., 2010). The high precipitation estimates are in agreement with models that show northern high latitudes as being 'ever-wet' or equable (Huber and Goldner, 2012), and contradicts isotopic evidence that reported a monsoonal climate signal.

Understanding the precipitation regimes and seasonality of the Arctic during this time in Earth's history may prove pivotal in understanding the direction of our changing modern climate. There is mounting evidence to suggest that changing climate will have drastic effects upon the world's fragile Arctic ecosystems (ACIA, 2005; Serreze and Barry, 2011). In order to understand the future implications of a changing climate and a warmer Arctic in Canada, a study of climate from the geologic past is essential and will assist the Eocene climate modeling community in refining their models (e.g., Huber and Caballero, 2011).

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Megaflora fossil site (no. morphotypes)	MAT °C ±2.1	WMMT °C ±2.5	CMMT °C ±3.4	LGS Months ±1.1	GSP cm ±31.7	3WET cm ±22.9	3DRY cm ±5.9	RH % ±8.6	SH g/kg ±1.7
Strathcona Fiord (15)	13.0	22.3	4.0	7.7	110.6	54.4	27.0	83.6	11.0
Split Lake (11)	14.4	24.4	4.6	8.4	96.5	39.1	31.3	84.2	13.3
Stenkul Fiord (25)	12.7	22.0	3.6	7.5	90.4	46.2	26.5	84.0	11.2

Table 2.1: CLAMP estimates which include mean annual temperature (MAT), warm month mean temperature (WMMT), cold month mean temperature (CMMT), length of growing season (LGS), growing season precipitation (GSP), three wettest months precipitation (3WET), three driest months precipitation (3DRY), relative humidity (RH), specific humidity (SH).

Megaflora fossil site (no. morphotypes)	MAT	MAP (LAA) cm/yr
Strathcona Fiord (15)	12.4 ± 3.8 12.1 ± 4.8	230 +99/-69 207 +174/-94
Split Lake (11)	10.9 ± 4.3 11.1 ± 4.8	228 +98/-69 206 +173/-94
Stenkul Fiord (25)	8.5 ± 2.6 9.5 ± 4.8	240 +104/-72 211 +178/-96

Table 2.2: LMA estimates of mean annual temperature (MAT), and LAA estimate of mean annual precipitation (MAP).

Note: MAT estimates were calculated from the classic LMA equation of Wing and Greenwood (1993), whereas the second estimate was calculated from the global LMA equation in Peppe et al. (2011). MAP estimates were calculated from the direct measurement approach of Wilf et al., (1998), whereas the second estimate was calculated from the global LAA equation in Peppe et al., (2011)

Stenkul Fiord Profile From Harrington et al. 2012	MAT °C	WMMT °C	CMMT °C	MAP cm/yr
Profile M above white sand marker bed	16.2 ± 3.6	21.5 ± 4.7	6.9 ± 5.4	117.0 ± 39.4
Profile M below white sand marker bed	17.0 ± 3.7	22.3 ± 3.9	9.2 ± 3.8	125.2 ± 33.0
Profile P above white sand marker bed	14.1 ± 5.9	21.6 ± 5.1	4.8 ± 8.0	115.0 ± 41.4
Profile P below white sand marker bed	14.4 ± 5.6	21.9 ± 4.8	4.9 ± 8.1	115.0 ± 41.3

Table 2.3: Bioclimatic Analysis estimates (this study) using palynoflora from Stenkul Fiord gathered by Harrington et al., (2012); which includes mean annual temperature (MAT), warm month mean temperature (WMMT), cold month mean temperature (CMMT), and mean annual precipitation (MAP).

Megaflora fossil site	MAP - GSP	Approximated Winter Precipitation Range (WP) cm
Strathcona Fiord	(230 +99/-69) – (110.6 ± 31.7) (207 +174/-94) – (110.6 ± 31.7)	80-187 59-239
Split Lake	(228 +98/-69) – (96.5 ± 31.7) (206 +173/-94) – (96.5 ± 31.7)	100-198 47-251
Stenkul Fiord	(240 +104/-72) – (90.4 ± 31.7) (211 +178/-96) – (90.4 ± 31.7)	110-230 56-267

Table 2.4: Approximated Winter Precipitation Range resulting from subtracting GSP from MAP and including all errors from CLAMP and LAA

Note: The first series of equations and WP range estimates are calculated using the results from the Wilf et al., (1998) LAA equation, whereas the second series of equations and WP range estimates are calculated using the results of the global LAA equation of Peppe et al., (2011)

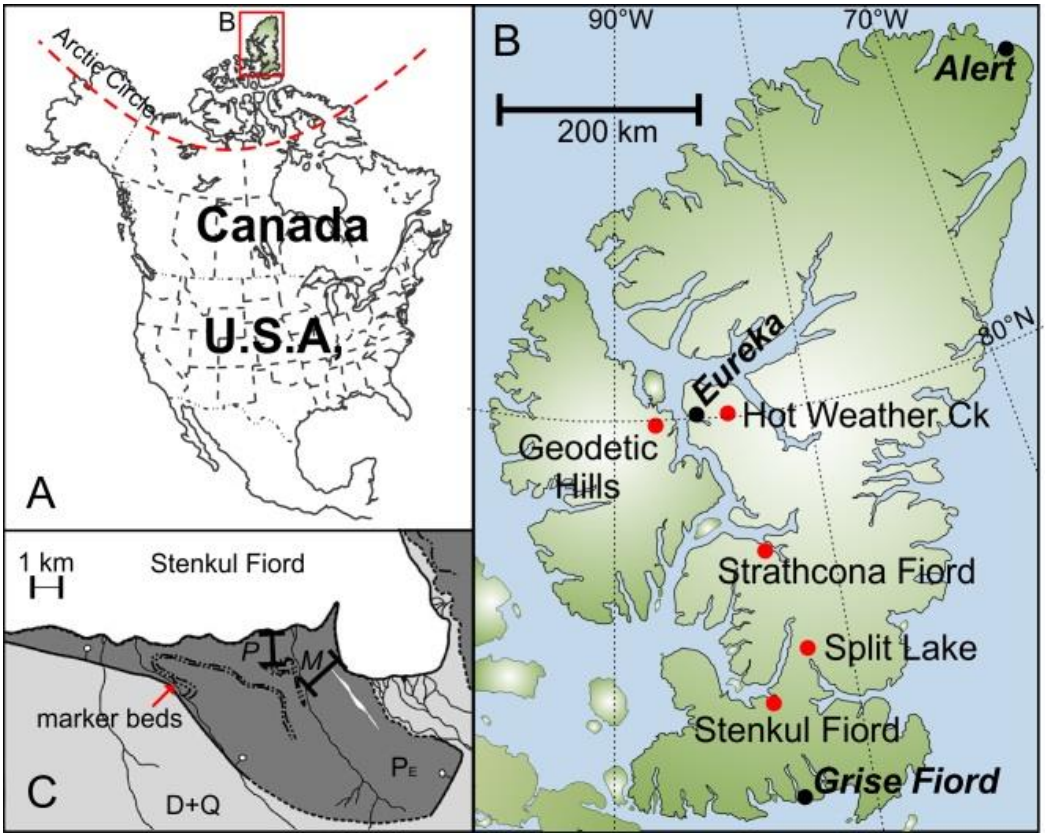

Figure 2.1. Location maps. A, North America showing position of Ellesmere Island; B, Ellesmere Island showing location of the 3 fossil localities and other sites mentioned in the text; C, detail of Stenkul Fiord showing main outcrop. PE, Paleogene Eureka Sound Group sediments; D+Q, Devonian rocks and undifferentiated drift. P and M, measured sections. Red dotted line represents the Arctic Circle. Adapted from Kalkreuth et al. (1998), Eberle and Greenwood (2012), and Harrington et al. (2012).

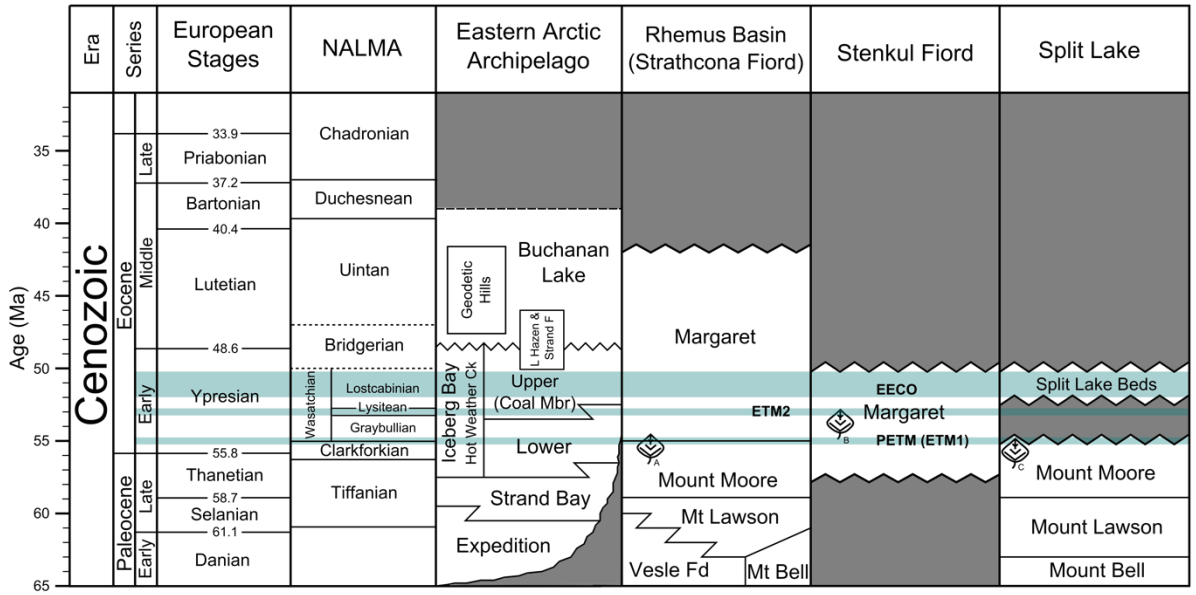

Figure 2.2. Early Paleogene lithostratigraphic chart that shows chronostratigraphic positions of the megafloras (A - Strathcona Fiord, B - Stenkul Fiord, and C - Split Lake) that are the primary focus of this study. The major early Eocene hyperthermals and climatic optimum (PETM, ETM2, and EECO) are shown as blue bars (modified from Eberle and Greenwood, 2012).

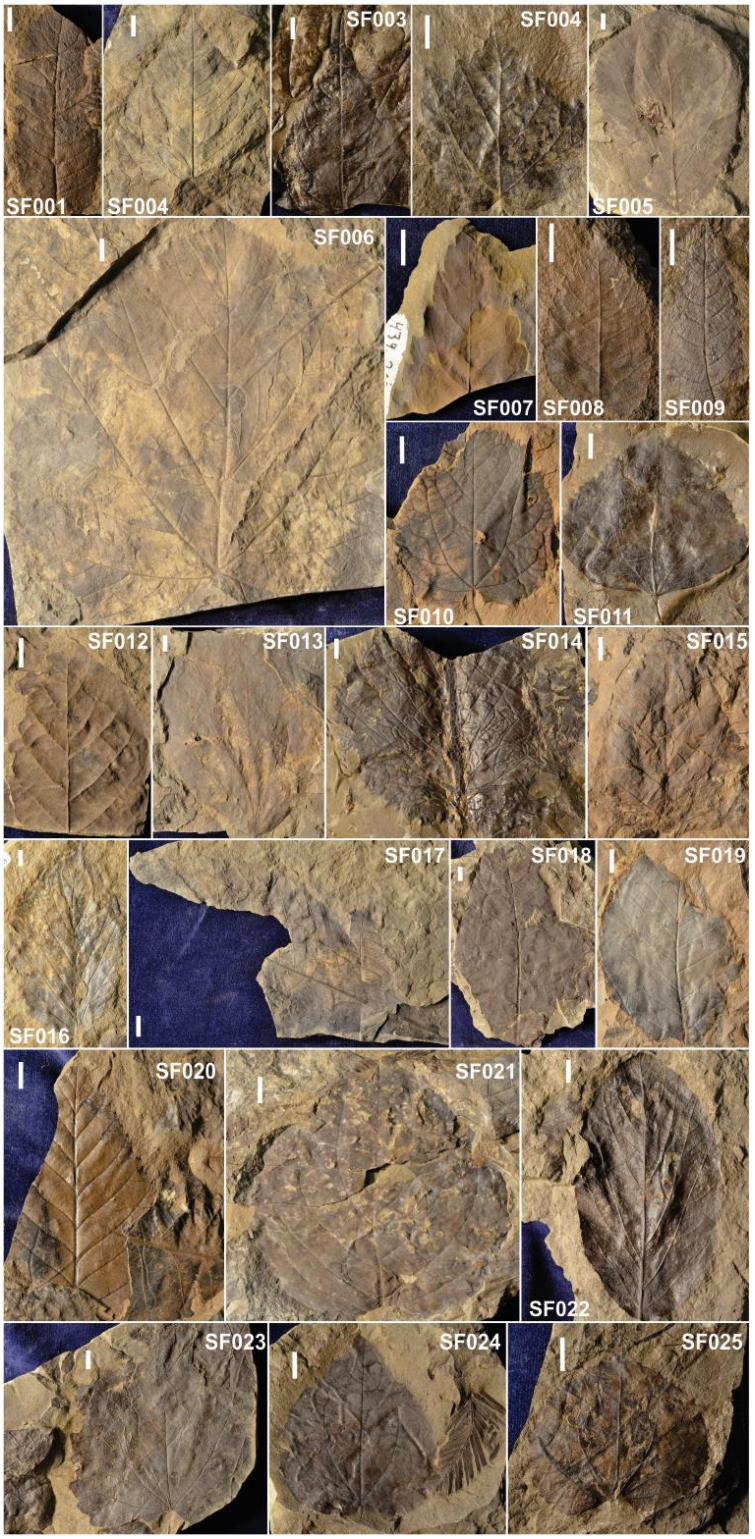

Figure 2.3. Representative specimens of the 25 leaf morphotypes from the Stenkul Fiord locality of Ellesmere Island. Morphotype descriptions and specimen list given in the online supplementary material. SF = Stenkul Fiord. All scale bars = 1 cm.

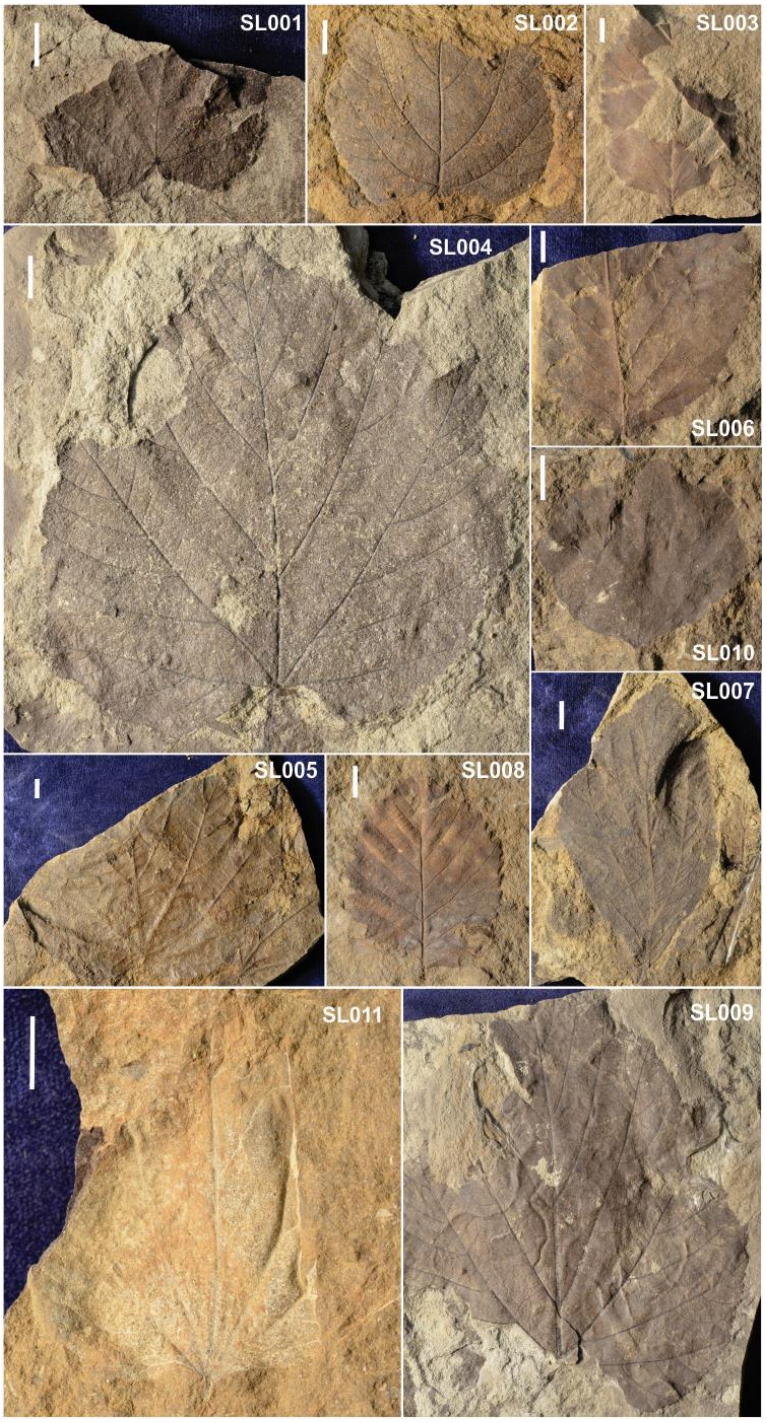

Figure 2.4. Representative specimens of the 11 leaf morphotypes from the Split Lake locality of Ellesmere Island. Morphotype descriptions and specimen list given in the online supplementary material. SL = Split Lake. All scale bars = 1 cm.

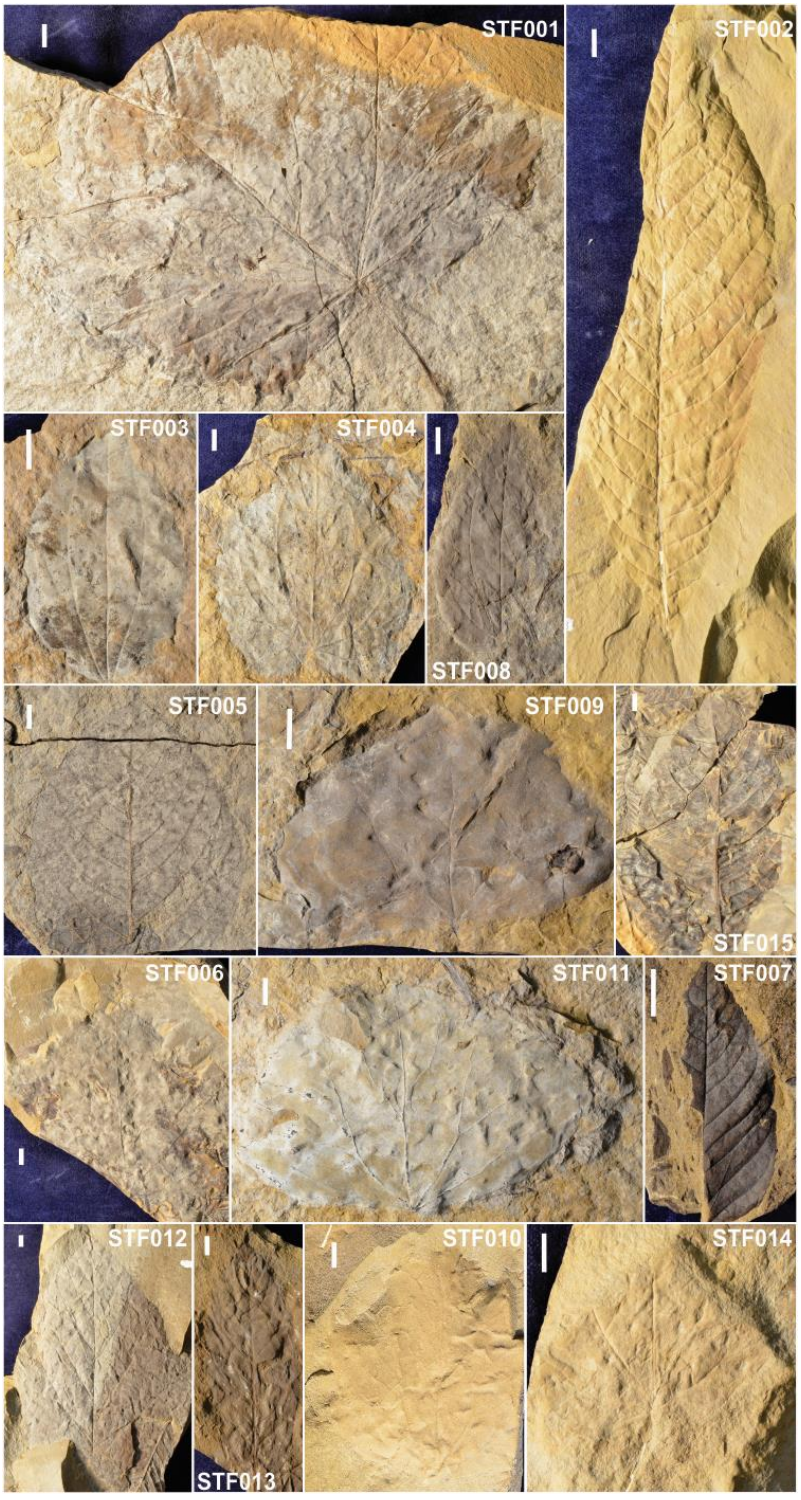

Figure 2.5. Representative specimens of the 15 leaf morphotypes from the Strathcona Fiord locality of Ellesmere Island. Morphotype descriptions and specimen list given in the online supplementary material. STF = Strathcona Fiord. All scale bars = 1 cm.

3. THE LATE PALEOCENE TO EARLY EOCENE ARCTIC MEGAFLORA OF ELLESMERE AND AXEL HEIBERG ISLANDS, NUNAVUT, CANADA

This paper is in press for publication in the journal *Palaeontographica Abteilung B* and adheres to the style and format required by that journal, and will be published as: WEST, C. K., GREENWOOD, D. R., & BASINGER, J. F. (in press): The late Paleocene to early Eocene Arctic megaflora of Ellesmere and Axel Heiberg islands, Nunavut, Canada. *Palaeontographica Abteilung B*

Abstract: The late Paleocene - **e**arly Eocene sediments of Ellesmere and Axel Heiberg islands, Nunavut, of the Canadian High Arctic contain a rich fossil flora and fauna. Although the megafloral fossils have been known for more than a century, limited descriptions of the fossil flora have been presented. Here, we provide a comprehensive morphotype catalogue of fossil plants from multiple localities from Ellesmere and Axel Heiberg islands that form a systematic framework for establishing an early Paleogene polar flora from High Arctic latitudes in Canada. Described are 62 'dicot' angiosperm morphotypes, three monocotyledonous angiosperms, 13 gymnosperms, and five pteridophyte morphotypes. This work presents a significant contribution to the understanding of north-polar diversity and environments during the warm greenhouse climate of the early Paleogene.

3.1 Introduction

Modern cold polar environments are an anomaly within Earth's history, as polar regions have been far more commonly warm – essentially ice-free – and wet than they have been cold and dry (e.g., WOLFE 1975, 1980; HERMAN & SPICER 1996; REES ET AL. 1999; WEIJERS ET AL. 2007; WEST ET AL. 2015). The late Paleocene to early Eocene sediments on Ellesmere and Axel Heiberg islands (Figure 3.1) preserve an extensive palaeontological record from the warmest interval of the Cenozoic (EBERLE & GREENWOOD 2012).

During the early Paleogene, the Canadian High Arctic was home to forests dominated by temperate deciduous hardwoods, conifers and ferns (BASINGER 1991; GREENWOOD & BASINGER 1994; MCIVER & BASINGER 1999; DOLEZYCH & ESTRADA 2012; WEST et al. 2015; DOLEZYCH et al. 2018); as well as a complex and unique polar fauna of alligators, snakes, turtles, large mammals, early primates, and terror birds (ESTES & HUTCHINSON 1980; MCKENNA 1980; DAWSON et al. 1993; EBERLE 2005; EBERLE et al. 2014; STIDHAM & EBERLE 2016). These polar forests existed during a warm greenhouse world when global temperatures were much higher than modern and the global climate system was punctuated by a series of superimposed short-lived hyperthermal events (e.g., the Paleocene-Eocene Thermal Maximum (PETM) ca. 56 Ma, and the Eocene Thermal Maximum 2 (ETM-2) ca. 53.7 Ma) ─ intense episodes of global warming that represent some of the warmest intervals of the Cenozoic (ZACHOS et al. 2008; SLUIJS et al. 2009; MCINERNEY & WING 2011; ANAGNOSTOU et al. 2016; WILLARD et al. 2019).

The fossil bearing strata on Ellesmere and Axel Heiberg islands were discovered by early Arctic explorers of the British Arctic Expedition (FEILDEN & DE RANCE 1878). The fossil plants recovered north-west of Cape Murchison on Ellesmere Island by Captain H.W Feilden of the British Arctic Expedition were compared to fossil flora from Spitsbergen by the eminent Swiss naturalist Oswald Heer, and subsequently described based on these comparisons (HEER 1878a). Although Heer himself had not visited Ellesmere Island due to continual ill health, he described the shales of Ellesmere Island as containing “rich botanical treasures” and lamented that Captain Feilden had made only two visits to the fossil beds (HEER 1878b, p. 66).

HEER (1878a) reported 26 megaflora taxa from Ellesmere Island, of which 18 could be found elsewhere in the Arctic zone. He noted that 17 plant species were shared with Spitsbergen and eight plant species with Greenland, all of which were at the time considered to be Miocene in age, and he concluded that the fossil bearing shales on Ellesmere Island must also be Miocene.

Since discovery and initial description over a century ago (e.g., FEILDEN & DE RANCE 1878; HEER 1878a; GREELY 1886; NATHORST 1915) the Canadian Arctic fossil megaflora has undergone only limited taxonomic revision. MCIVER & BASINGER (1999) have provided the most recent overview of the early Paleogene fossil megaflora from Ellesmere and Axel Heiberg islands. Nevertheless, much work has been done on the interpretation of these fossil plants to answer questions of palaeoecological and palaeoclimatic importance (e.g., GREENWOOD & BASINGER 1993, 1994; BASINGER et al. 1994; MCIVER & BASINGER 1999; GREENWOOD et al. 2010; WEST et al. 2015).

Presented here is the first detailed analysis, description, and characterization of the late Paleocene to early Eocene fossil flora from Ellesmere and Axel Heiberg islands, which has been based on fossil collections collected primarily during expeditions led by J. F. Basinger and L. J. Hickey during the 1980's, 1990's, and early 2000's. The fossil flora has been evaluated, categorized, and described using the morphotype method, where each 'morphotype' – a species-like taxonomic entity – is morphologically differentiated but not necessarily assigned to a Linnean taxon (e.g., ELLIS et al. 2009). Where possible, the fossil plants have been referred to taxa previously described from the late Paleocene and early Eocene and assigned taxonomic identities when possible. Sixty-two 'dicot' angiosperm morphotypes are described and figured. Additionally, three monocotyledonous angiosperms, 13 gymnosperms, and five pteridophyte morphotypes are also described and figured. It should be noted that the rich and distinctive middle Eocene deposits of the Buchanan Lake Formation of Axel Heiberg Island, which were included in the overview by MCIVER & BASINGER (1999) and subject to limited taxonomic investigation (e.g. LEPAGE & BASINGER 1991, 1995; LIU & BASINGER 2000, 2009; LEPAGE 2001, 2003; KOTYK et al. 2003; JAHREN 2007), are not included in this report but will be the subject of a subsequent study.

3.2 Age and geologic setting

The late Paleocene–early Eocene sediments on Ellesmere and Axel Heiberg islands were deposited into the Sverdrup Basin and form part of the Eureka Sound Group (RICKETTS 1994). During the early Paleogene, these islands were located at a palaeolatitude of approximately ~75-80°N, or about 2° south of their present location (IRVING & WYNN 1991).

The sediments of the Eureka Sound Group have been the subject of considerable study and interpretation, resulting in multiple nomenclatural schemes, often developed simultaneously (e.g., WEST et al. 1977, 1981; MIALL 1986, 1991; RICKETTS 1986, 1994; HARRISON et al. 1999). The schemes of MIALL (1986) and RICKETTS (1986) are the most commonly used. MIALL (1986) recognized nine formation-rank units, including: the Mount Bell, Vesle Fiord, Mount Lawson, Mount Moore, Cape Back, Cape Lawrence, Mokka Fiord, Margaret, and Boulder Hills formations. The nomenclature for the Eureka Sound Group developed by RICKETTS (1986) includes: the Expedition, Strand Bay, Iceberg Bay, and the Buchanan Lake formations. These formations are considered to span the latest Cretaceous to the early Oligocene (MIALL 1986, 1991). This study employs the nomenclatural scheme developed by MIALL (1986), as it is in most common use, although the correlative nomenclature of RICKETTS (1986), mostly commonly utilized for strata on Axel Heiberg Island, will be mentioned where appropriate.

Although all these formations are considered fossiliferous to some extent, the fossil plants – leaves and reproductive organs or 'megaflora' – of the Mount Lawson, Mount Moore, and Margaret, and to a lesser extent the Mokka Fiord, and the geographically restricted Cape Back, and Cape Lawrence formations (Figure 3.2) are the focus of this study.

The Mount Lawson Formation (= Strand Bay Formation of RICKETTS 1986) has been analyzed palaeomagnetically and correlated with chrons 25 and 26 (Figure 3.2) (TAUXE & CLARK 1987). Zircons recovered from the Mount Lawson Formation exposed at Split Lake were dated using U–Pb SHRIMP analysis and yielded an age of 53.9 ± 3 Ma, late Paleocene to early Eocene (REINHARDT et al. 2013). The palaeomagnetic data coupled with the U–Pb derived

age suggest the age of the Mount Lawson Formation should be regarded as late Paleocene to early Eocene.

The Mount Moore Formation at Strathcona Fiord includes diagnostic fossils, including shark teeth (*Odontaspis*), teleost fish otoliths (WEST et al. 1977), a bivalve previously recorded from the Thanetian stage (MARINCOVICH & ZINSMEISTER 1991), foraminifera similar to those described from the Paleocene Agatdal Formation of Western Greenland (HANSEN 1970; RICKETTS 1994; HARRISON et al. 1999), and palynomorphs that first appear in chron 25n but may be as young as 24r (HARRISON et al. 1999).

Palaeomagnetic and biostratigraphic dating of the Mount Moore Formation at Strathcona Fiord suggest a Paleocene age (TAUXE & CLARK 1987; MARINCOVICH & ZINSMEISTER 1991); however, the U–Pb derived age of the Mount Lawson Formation from Split Lake (i.e., 53.9 ± 3 Ma) may be used to expand the age of the Mount Moore Formation, as the Mount Lawson Formation is conformably overlain by the Mount Moore Formation in the Split Lake area (MIALL 1986; REINHARDT et al. 2013), which suggests that the Mount Moore Formation should be regarded as late Paleocene to early Eocene in age.

The lower part of the Margaret Formation (= Coal Member of the Iceberg Bay Formation of RICKETTS 1986) is late Paleocene (Thanetian) to early Eocene (Ypresian) based on palynology and on fossil vertebrates using the North American Land Mammal Ages (WEST et al. 1977, 1981; MARINCOVICH et al. 1990; DAWSON et al. 1993; KALKREUTH et al. 1993, 1996; HARRISON et al. 1999; EBERLE & GREENWOOD 2012; EBERLE & EBERTH 2015). Zircon crystals have also been recovered from prominent ash layers in the Margaret Formation at Stenkul Fiord that provide an age of 53.7 ± 0.6 Ma from U–Pb SHRIMP analysis, that is, early Eocene (REINHARDT et al. 2013, 2017).

The Mokka Fiord Formation is a geographically extensive formation and can be found across both Ellesmere and Axel Heiberg Islands, and is typically considered equivalent in age to both the Mount Moore and the Margaret formations (MIALL 1991). The Cape Back and Cape

Lawrence formations are restricted to the Judge Daly Promontory. The Cape Back was assigned a late Paleocene age by MIALL (1982) based on megaflora. The Cape Lawrence Formation is also considered late Paleocene based on fossil megaflora, but as it rests unconformably upon the Cape Back Formation it may also be younger (MIALL 1991; HARRISON et al. 1999).

The depositional environment of these formations has been interpreted as proximal delta-front to delta-plain environments, with abundant channels and coal swamps with rare instances of open marine conditions (MIALL 1986, 1991; RICKETTS 1986, 1994).

3.3 Materials and methods

The bulk of the fossils used for this study are housed at the University of Saskatchewan and are part of the University of Saskatchewan Paleobotanical Collection (USPC), while additional fossils were integrated and described from those housed at the Yale Peabody Museum (YPM). The collections have been derived from numerous localities across Ellesmere and Axel Heiberg islands (northernmost part of the Canadian Arctic Archipelago), northern Nunavut, Canada, between latitudes 77°N and 82°N (Figure 3.2).

Fossil specimens are designated by both locality and specimen numbers that are linked to locality data, specimen information, and repository. USPC specimens are preceded by a repository designation attached to a locality number (e.g., USPC 435), followed by a specimen number (e.g., 2839). YPM specimens follow a similar format, except the repository identifier precedes a letter prefix, in this case PB, then a six-digit specimen number (e.g., YPM PB 169880), followed by a four-digit locality number (e.g., 7936). Locality information, when listed separately, is preceded by the repository acronym (i.e., USPC or YPM) where the locality data is held. Fossils collected during the 2017 field season are the property of the Nunavut government, and will eventually be stored at the Canadian Museum of Nature (CMN). These specimens are listed with their CMN Nunavut Paleobotany (NUPB) specimen numbers (e.g., NUPB 656).

The fossils used in this study were collected from 8 principal locality regions (Table 3.1). Geological maps of these regions that correspond to boxes 1-5 on Figure 3.1 have been included (Figures 3.3-3.7), as well as a master legend of geological formations and other data found on the maps (Figure 3.8). The locality zones include 20 major localities that can be further subdivided into 121 sub-localities, each with a unique locality number (see appendix A). Additional information about the localities and corresponding sub-localities can be found in appendix A.

The University of Saskatchewan specimens were recovered primarily from fluvial sand, crevasse splay and swamp mudstone facies, and were collected on numerous expeditions from 1982 to 2004 led by J. F. Basinger, with additional specimens collected by C. K. West in 2017. The YPM fossil floras and locality data were collected from similar sedimentary facies during the 1970's to 80's by the late L. J. Hickey and others.

3.3.1 Fossil photos and leaf trace outlines

Fossils were photographed using digital SLR Nikon D5100 & D5300 cameras and were taken as high-resolution JPEGs. Images of morphotype exemplars were imported into Adobe© Photoshop CS6. Transparency and line tools were used to trace the morphotype exemplars, with images inverted to allow for finer detail to be traced. Leaf tracings were used to assist in analysis and confirmation of architectural characteristics used for morphotype organization and assignment. In some cases, the contrast and brightness of photos have been adjusted to enhance the quality of detail visible.

3.3.2 Taxonomy and morphotypes

The late Paleocene–early Eocene fossil megaflora of Ellesmere and Axel Heiberg islands were sorted into morphologically distinct groups of specimens, or morphotypes. Morphotypes are morphological groupings that may parallel traditional biological species concepts, but that have no formal taxonomic status (JOHNSON 1989; PEPPE et al. 2008; ELLIS et al. 2009). Thus,

the morphotype system can be used to develop a rigorous classification system unique to a fossil locality, geological unit, or basin that is independent of the traditional Linnean framework (JOHNSON 1989; PEPPE et al. 2008; MAXBAUER et al. 2013).

The morphotype system has an advantage over Linnean taxonomy in that traditional taxonomic and systematic descriptions are often challenging and time-consuming processes, whereas, the morphotype system allows for fossil floras to be rapidly and rigorously classified (JOHNSON 1989; PEPPE et al. 2008). Thereby, allowing both palaeoecological and palaeoclimatological analyses can be applied to a flora before a complete taxonomic assessment occurs (e.g., WEST et al. 2015; LOWE et al. 2018). Although established morphotypes may not necessarily parallel previously described taxa, nevertheless, as descriptions are improved, or as new information becomes available, morphotypes may be referred to existing or new Linnean taxa (please see PEPPE et al. 2008 for a more complete review of the morphotype system).

Morphotypes for this study were described following the methodology and terminology presented by ELLIS et al. (2009), and following a model similar to PEPPE et al. (2008). Morphotypes were assigned "morphotype numbers", a numerical designation used to distinguish specific fossils, or groups of fossils, within the flora. Specific to this study, the morphotype number consists of a 3-letter prefix and a number, the letter prefix is based on the region (i.e., the Canadian Arctic Flora, or CAF). Morphotype exemplars were established for each morphotype, which serve as reference specimens for each morphotype, and may be later changed if better specimens are found (JOHNSON 1989; PEPPE et al. 2008).

It should be noted that the numbering of morphotypes during the present study was an evolutionary process, and many numbers were eliminated as fossils were grouped in to more representative morphotypical units. Thus, "morphotype numbers" assigned to morphotypes reflect an identifying code rather than a numerical tally of types.

In general, primary and secondary venation was visible for the majority of fossil leaf specimens from Ellesmere and Axel Heiberg islands, whereas third-order venation was less

commonly preserved or visible, while fourth- and fifth-order venation patterns were rarely preserved on specimens. Venation patterns were therefore typically given dominance over other architectural characters (e.g., size, shape, margin, base and apex) in sorting specimens into their constituent morphotypes, as venation systems are typically more stable than other architectural characters, and thus may be more taxonomically useful (DILCHER 1974; HICKEY 1973, 1978; HICKEY & WOLFE 1975). In some cases, however, deviations or gross dissimilarities do occur, and these other architectural characters are then invoked for sorting processes.

As noted above, for descriptive purposes the terminology developed by ELLIS et al. (2009) has been employed; however, in the case of reproductive remains (e.g., fruits, flowers, cones, and seeds), more traditional taxonomic descriptive methods and terminology have been employed. Nevertheless, these too have been grouped into morphotypes and described as such. This non-traditional, blended methodology has been adopted in order to provide as robust and comprehensive a catalogue of late Paleocene to early Eocene fossil megaflora from Ellesmere and Axel Heiberg islands as possible, as efficiently as possible, in order to facilitate additional future palaeoecological and palaeoclimatlogical analyses that require a robust ordinal framework.

3.4 Systematics

The results of this study have produced 83 plant megaflora morphotype descriptions from the Canadian Arctic Flora (CAF), of these 65 are angiosperm (62 “dicots” and 3 monocotyledonous) morphotypes. The remaining 18 megafloral morphotypes are comprised of 13 gymnosperms and 5 pteridophytes. The complete systematic list can be found below in section 3.4.1. Morphotypes are also listed in sequence and grouped by general geographic localities as found in Table 3.1.

No new taxa have been formally described or established during this study; however, studies focused on the establishment of new taxa will be the basis of future work on the early

Paleogene fossil flora of Ellesmere and Axel Heiberg islands. Morphotypes described as *incertae sedis* are grouped into classes (i.e., ferns, gymnosperms, angiosperms) that likely best represent their possible affinities and are organized by organ (i.e., leaf, infructescence, fruit, seeds, and unknown botanical structures) for clarity.

When possible the morphotypes developed have been referred to, or assigned affinities to, previously established genera and species. In cases where affinities are uncertain the assignment may be preceded by cf. (= "compares to") or aff. (= similar to, but likely representing a new taxon).

Where no comparisons or affinities can be provided, the morphotype has been designated with indeterminate family, genus, and species, which effectively places the morphotype as *incertae sedis*. Higher order classification follows RUGGIERO et al. (2015), whereas taxonomic affinities and assignments at the order level and below follow PPG I (2016) for ferns and horsetails (Class Polypodiopsida), CHRISTENHUSZ et al. (2011) for gymnosperms, and APG IV (2016) for angiosperms.

3.4.1 Systematic List

Polypodiopsida
- Equisetales
  - Equisetaceae
    - *Equisetum* sp. (CAF-082)
- Osmundales
  - Osmundaceae
    - *Osmunda macrophylla* PENHALLOW (CAF-119)
- Salviniales
  - Salviniaceae
    - *Azolla* sp. (CAF-150)
    - *Salvinia* cf. *S. preauriculata* BERRY (CAF-084)
- Cyatheales
  - Dicksoniaceae

Coniopteris blomstrandii (HEER) KVAČEK et MANUM (CAF-081)

Ginkgoopsida

Ginkgoales

Ginkgoaceae

Ginkgo adiantoides (UNGER) HEER (CAF-110)

Pinopsida

Pinales

aff. Pinaceae

gen. indet. sp. indet. (CAF-115)

Cupressales

Cupressaceae

cf. *Cunninghamia* sp. (CAF-109)

Metasequoia occidentalis (NEWBERRY) CHANEY (CAF-107)

Glyptostrobus nordenskioldii (HEER) BROWN *(*CAF-108)

Elatocladus cordillera CHRISTOPHEL (CAF-111)

Thuja polaris MCIVER et BASINGER (CAF-135)

Cupressinocladus sp. 1 (CAF-121)

Cupressinocladus sp. 2 (CAF-136)

gen. indet. sp. indet. (CAF-085)

gen. indet. sp. indet. (CAF-148)

gen. indet. sp. indet. (CAF-152)

gen. indet. sp. indet. (CAF-139)

Magnoliopsida

Magnoliids

Magnoliales

aff. Magnoliaceae

Magnolia sp. (CAF-102)

Monocots

Zingiberales

Zingiberaceae

Zingiberopsis cf. Z. *isonervosa* HICKEY (CAF-118)

Incertae sedis

Incertae sedis

gen. indet. sp. indet. (CAF-096)

gen. indet. sp. indet. (CAF-133)

Eudicots

Proteales

Nelumbonaceae

cf. *Nelumbo* sp. (CAF-072)

Platanaceae

Macginitiea aff. *M. nobilis* (NEWBERRY) MANCHESTER (CAF-080)

Macginicarpa cf. *M. manchesteri* PIGG et STOCKEY (CAF-126)

Platanus sp. (CAF-128)

Trochodendrales

Trochodendraceae

Nordenskioeldia borealis HEER (CAF-112)

Tetracentron cf. *T. hopkinsii* PIGG, DILLHOFF, DEVORE et WEHR (CAF-040)

Core Eudicots

Saxifragales

Cercidiphyllaceae

Archeampelos cf. *A. acerifolia* (NEWBERRY) MCIVER et BASINGER (CAF-034)

Nyssidium arcticum (HEER) ILJINSKAJA (CAF-088)

Trochodendroides arctica (HEER) BERRY (CAF-035)

Trochodendroides curvidens (HEER) GOLOVNEVA et BUDANTSEV (CAF-036)

Trochodendroides crenulata (HEER) KVAČEK, MANUM et BOULTER (CAF-021)

Trochodendroides richardsonii (HEER) KRYSHTOFOVICH (CAF-098)

gen. indet. sp. indet. (CAF-144)

Rosids

Vitales

aff. Vitaceae

Vitiphyllum cf. *V. sewardii* BOULTER et KVAČEK (CAF-004)

Fabids

Fagales

Betulaceae

Alnus cf. *A. parvifolia* (BERRY) WOLFE et WEHR (CAF-061)

Alnus sp. (CAF-091)

cf. *Paracarpinus* sp. (CAF-031)

Corylites hebridicus SEWARD et HOLTTUM (CAF-129)

Craspedodromophyllum cf. *C. malgrenii* (HEER) GOLOVNEVA (CAF-054)

Fagaceae

Fagopsiphyllum cf. *F. groenlandicum* (HEER) MANCHESTER (CAF-065)

Juglandaceae

cf. '*Carya*' *antiquorum* NEWBERRY (CAF-014)

Myricaceae

Comptonia sp. (CAF-069)

Incertae sedis

Ushia cf. *U. olafsenii* (HEER) BOULTER et KVAČEK (CAF-027)

Rosales

Rosaceae

cf. *Crataegus* sp. 1 (CAF-101)

cf. *Crataegus* sp. 2 (CAF-127)

cf. *Sorbaria* aff. *S. wahrhaftigii* WOLFE et WEHR (CAF-079)

Ulmaceae

Ulmus ulmifolia (SCHLOEMER-JÄGER) BUDANTSEV (CAF-012)

Malvids

Sapindales

Sapindaceae

Aesculus longipedunculus SCHLOEMER-JÄGER (CAF-038)

Incertae sedis

Incertae sedis

Incertae sedis

Averrhoites cf. *A. affinis* (NEWBERRY) HICKEY (CAF-067)

aff. *Celastrinites* sp. (CAF-131)

cf. *Cornophyllum* sp. (CAF-032)

Macclintockia sp. (CAF-149)

Quereuxia angulata (NEWBERRY) KRYSHTOFOVICH (CAF-105)

gen. indet. sp. indet. (CAF-016)

gen. indet. sp. indet. (CAF-024)

gen. indet. sp. indet. (CAF-025)

gen. indet. sp. indet. (CAF-033)

gen. indet. sp. indet. (CAF-063)

gen. indet. sp. indet. (CAF-070)

gen. indet. sp. indet. (CAF-073)

gen. indet. sp. indet. (CAF-100)

gen. indet. sp. indet. (CAF-103)

gen. indet. sp. indet. (CAF-104)

gen. indet. sp. indet. (CAF-130)

gen. indet. sp. indet. (CAF-132)

gen. indet. sp. indet. (CAF-134)

gen. indet. sp. indet. (CAF-151)

gen. indet. sp. indet. (CAF-086)

gen. indet. sp. indet. (CAF-123)

gen. indet. sp. indet. (CAF-124)

gen. indet. sp. indet. (CAF-137)

gen. indet. sp. indet. (CAF-146)

gen. indet. sp. indet. (CAF-147)

gen. indet. sp. indet. (CAF-093)

gen. indet. sp. indet. (CAF-138)

gen. indet. sp. indet. (CAF-142)

gen. indet. sp. indet. (CAF-143)

gen. indet. sp. indet. (CAF-145)

gen. indet. sp. indet. (CAF-140)

gen. indet. sp. indet. (CAF-141)

3.5 Morphotype catalogue and descriptions of taxa

Polypodiopsida

Order Equisetales

Family EQUISETACEAE

Genus *Equisetum* L.

Equisetum sp.

Morphotype CAF-082

Pl. 1, Figs. 1–9

Morphotype exemplar: USPC 715-2230

Location: USPC 22, 101, 102, 104, 105, 111, 162, 168, 198, 251, 261, 361, 435, 442, 708, 712, 715, 753, 759

Description: Aerial stems incomplete, unbranched, stems grooved and ridged longitudinally; stem fragments up to 8 mm wide, up to 50 mm long, stems appear to narrow distally; internodal lengths up to 32 mm; apparent branches 4 mm wide, up to 40 mm long but incomplete. Leaves whorled at nodes, fused proximally into collars, 16-30 leaves per collar; unfused portion of leaves up to 14 mm long; apex acute to acuminate, appear appressed. Rhizomes 5-14 mm wide, up to 120 mm long; adventitious roots may be present at nodes; roots 5-7 mm long but incomplete. Probable tubers elliptic to obovate, up to 32 mm long and 10 mm wide; tubers may be found attached to nodes in whorls of up to 5.

Remarks: This morphotype is described from sterile material that strongly resembles fossil material previously referred to the extant genus *Equisetum* L. from both mid- and high-latitude fossil localities from the early Paleogene in North America, Greenland, Svalbard, and the Isle of Mull (e.g., HEER 1868, 1869, 1878a; HOLLICK 1936; BELL 1949; SCHLOEMER-JÄGER 1958; BROWN 1962; HICKEY 1977; SCHWEITZER 1980; BOULTER & KVAČEK 1989; MCIVER & BASINGER 1989b, 1993; BUDANTSEV & GOLOVNEVA 2009).

Equisetum arcticum HEER, a fossil-species originally described from Spitsbergen and

common to high-latitude early Paleogene fossil localities (e.g., HOLLICK 1936; BELL 1949; SCHLOEMER-JÄGER 1958; BUDANTSEV & GOLOVNEVA 2009), is known primarily from aerial stems, leaf collars, rhizomes, and tubers (MCIVER & BASINGER 1993). Previous authors have noted that *Equisetum arcticum* is inadequately described and the material used is typically poorly preserved and does not have sufficient characters to adequately describe a species (BROWN 1962; BOULTER & KVAČEK 1989; MCIVER & BASINGER 1993). Following BROWN (1962) and BOULTER & KVAČEK (1989), this morphotype is referred to *Equisetum* sp. as the architectural characters of the fossil specimens (e.g., stems, leaf collars, rhizomes, and tubers) are insufficient to justify a specific assignment.

Fossil remains referred to *Equisetum* are common in most Late Cretaceous and early Cenozoic plant fossil assemblages in the Northern Hemisphere (MCIVER & BASINGER 1989).

Order Osmundales

Family OSMUNDACEAE

Genus *Osmunda* L.

Osmunda macrophylla PENHALLOW 1908

Morphotype CAF-119

Pl. 1, Fig. 10

Morphotype exemplar: USPC 105-4717

Localities: USPC 22, 105, 753

Description: Frond bipinnate, pinna opposite to subopposite, rachis 1-1.5 mm wide, up to 100 mm long but incomplete. Pinna rachis 1 mm wide, up to 95 mm long but incomplete. Pinnules alternate, narrow-ovate, up to 30 mm long, up to 12 mm wide; apex obtuse; base truncate; pinnule margin erose or weakly serrate but may appear entire; teeth when present regularly spaced; tooth apex acute to obtuse; proximal pinnules attached to rachis by short stalk, distal pinnules appear sessile, terminal pinnule appears lobed. Venation open dichotomous; midvein stout, continuous toward apex; secondary veins dichotomize once or twice before reaching

margin.

Remarks: This morphotype was described from sterile fronds and strongly resembles fossil material previously referred to *Osmunda macrophylla* PENHALLOW, a fossil fern reported from many mid- and high-latitude early Paleogene fossil localities (e.g., PENHALLOW 1908; BELL 1949; BROWN 1962; HICKEY 1977; BOULTER & KVAČEK 1989; MCIVER & BASINGER 1993; BUDANTSEV & GOLOVNEVA 2009).

Osmunda was widely distributed in the northern temperate floras of Europe, Russia, and North America during the Paleogene (AKHMETIEV 2007; BUDANTSEV & GOLOVNEVA 2009).

Order Salviniales

Family SALVINIACEAE

Genus *Azolla* LAMARCK

Azolla sp.

Morphotype CAF-150

Pl. 1, Fig. 11

Morphotype exemplar: USPC 370-3823

Localities: USPC 370

Description: Leafy stems sterile, branched, up to 7.5 mm in length but incomplete, branching appears alternate, stems bear multiple leaves. Leaves appear alternate, sessile, presence of lobing could not be determined; leaves overlap the succeeding leaf; leaves ovate about 1 mm long, ≤ 1 mm wide; base obtuse; apex obtuse; margin untoothed; venation not observed. Sporangia not known.

Remarks: This morphotype resembles sterile fossil foliage referred to *Azolla* LAMARCK reported from early Paleogene localities in Canada (e.g., SWEET & CHANDRASEKHARAM 1973; MCIVER & BASINGER 1993; HOFFMAN & STOCKEY 1994: COLLINSON et al. 2017). The specimens recovered from Ellesmere Island are limited in number, and as the delineation of *Azolla* species requires reproductive material (COLLINSON et al. 2017), the specific affinity of this morphotype

remains unresolved.

Fossil *Azolla* has been reported from early Paleogene mid-latitude localities (e.g., ARNOLD 1955; GREENWOOD et al. 2005, 2016; MOSS et al. 2005; ARCHIBALD et al. 2011; MATHEWES et al. 2016; DILLHOFF et al. 2013; COLLINSON et al. 2017) and Russia (AHKMETIEV 2007, 2010), but is unknown from other high-latitude localities such as Alaska, Greenland, and Svalbard. *Azolla* appears to have been common in some settings in the Canadian Arctic in the middle Eocene (e.g., BRINKHUIS et al. 2006; COLLINSON et al. 2009, 2010; VAN DER BURGH et al. 2013; NEVILLE et al. 2019).

Genus *Salvinia* SÉG.

Salvinia cf. *S. preauriculata* BERRY 1925

Morphotype CAF-084

Pl. 1, Fig. 12

Morphotype exemplar: YPM PB 169880-848

Localities: YPM 848

Description: Leaflets found singly, up to 10 mm long but incomplete, up to 10 mm wide, oblong or ovate, appears symmetrical, waxy; apex angle obtuse, apex shape rounded; margin untoothed. Primary venation pinnate-like, midvein strong; secondary venation not observed. Probable papillae bases appear as points of depression, up to 1.5 mm in diameter, regularly spaced; papillae appear orientated and elongated laterally away from midrib.

Remarks: This morphotype resembles fossils referred to *Salvinia preauriculata* BERRY from the early Eocene Golden Valley Formation (BERRY 1925; HICKEY 1977); however, as the morphotype was described from several incomplete specimens the specific affinity remains tentative.

Salvinia SÉG. and *Salvinia*-like fossils are well known from the fossil record and have been reported from early Paleogene localities in North America and Russia (see COLLINSON 2001 and references therein; AHKMETIEV 2007), but are unknown from early Paleogene high-

latitude localities.

Order Cyatheales

Family DICKSONIACEAE

Genus *Coniopteris* A. T. BRONGNIART in A. C. V. D. D'ORBIGNY

Coniopteris blomstrandii (HEER 1868) KVAČEK et MANUM 1993

Morphotype CAF-081

Pl. 1, Fig. 13, Pl. 2, Fig. 1–2.

Morphotype exemplar: USPC 759-2202

Localities: USPC 22, 175, 275, 753, 759

Description: Pinnae incomplete, sterile, up to 86 mm long, wide. Pinnules alternate, pinnatifid, up to 13 mm long, up to 6 mm, lobed; pinnule apex acute; margin crenate; teeth appear regular, apex rounded, sinus acute. Venation open dichotomous.

Remarks: This morphotype resembles sterile foliage from Spitsbergen referred to the fossil-species *Coniopteris blomstrandii* (HEER) KVAČEK et MANUM (KVAČEK & MANUM 1993; BUDANTSEV & GOLOVNEVA 2009). Similar fossil foliage has been previously referred to the genus *Dennstaedtia* BERNHARDI, but KVAČEK & MANUM (1993) noted that many of these assignments were based on sterile foliage and may be in error. In cases where only sterile foliage could be found, KVAČEK & MANUM (1993) recommended using a fossil-genus (i.e., *Coniopteris* A. T. BRONGNIART in A. C. V. D. D'ORBIGNY) rather than an extant genus, a format followed here.

Coniopteris blomstrandii (= *Dennstaedtia blomstrandii* (HEER) HOLLICK = *Sphenopteris blomstrandii* HEER) has been reported from Russia, Alaska, the Isle of Mull, Svalbard, and Greenland (HEER 1868, 1874; HOLLICK 1936; BOULTER & KVAČEK 1989; KVAČEK & MANUM 1993; AHKMETIEV 2007; BUDANTSEV & GOLOVNEVA 2009); *Dennstaedtia americana* KNOWLTON, a fossil fern architecturally similar to *Coniopteris*, has been reported from contemporaneous mid- and high-latitude deposits (e.g., BROWN 1962; WOLFE 1966; MCIVER &

BASINGER 1993).

The fern *Coniopteris blomstrandii* has been considered a common element of the swamp forests that occupied northern latitudes during the Paleocene (BOULTER & KVAČEK 1989), and is now shown to extend from the late Paleocene to early Eocene palaeoarctic forests in Canada.

GYMNOSPERMS

Ginkgoopsida

Order: Ginkgoales

Family GINKGOACEAE

Genus *Ginkgo* L.

Ginkgo adiantoides (UNGER 1850) HEER 1878a

Morphotype CAF-110

Pl. 2, Fig. 15

Morphotype exemplar: USPC 111-4886

Localities: USPC 111, 163, 262

Description: Leaves flabellate, approximately 50-80 mm wide, 40-60 mm long. Base angle obtuse, base shape cuneate or decurrent; margin entire, occasionally undulate, typically notched medially; medial notch typically 1-3 mm deep. Venation strongly parallel, typically branched dichotomously; veins typically 0.5-1.0 mm apart or less, 12-16 veins/cm. Petiole about 2-3 cm long, swollen near laminar attachment point, narrows proximally.

Remarks: This morphotype was described from a limited number of specimens that strongly resemble fossil material previous referred to *Ginkgo spitsbergensis* MANUM from the Ravenscrag Formation, Saskatchewan, Canada (MCIVER & BASINGER 1993). This morphotype also shares some similarities with modern *Ginkgo biloba* L., such as the undulate leaf margin, a medial notch in the leaf margin, and the open dichotomous venation.

Ginkgo spitsbergensis was first described from leaf cuticle using transmitted light (MANUM 1966), a fossil character that is not available in the Ellesmere Island specimens. DENK

& VELITZELOS (2002) concluded from cuticular studies and architectural elements of both fossil and extant *Ginkgo* L. leaves that some early Paleogene fossil *Ginkgo* species (e.g., *Ginkgo spitsbergensis* and *Ginkgo wyomingensis* MANUM), should be considered conspecific with *Ginkgo adiantoides* (UNGER) HEER.

DENK & VELITZELOS (2002) observed that the differences in leaf cuticle and leaf architecture were subtle and may have been the result of natural ecological and intraspecific variation. Thus, the taxonomic significance of cuticular morphology in early Paleogene *Ginkgo* may be less significant than previously thought (DENK & VELITZELOS 2002); however, there remains some disagreement on this point (see GOLOVNEVA 2010). Regardless, it would seem most appropriate to refer this morphotype to *Ginkgo adiantoides*, as this name is typically used for *Ginkgo* leaves with entire margins and without preserved cuticle (GOLOVNEVA 2010).

Fossil forms of *Ginkgo* were widespread during the Late Cretaceous and Paleogene and have been described for the Arctic Paleogene from sites in Alaska, the Isle of Mull, Svalbard, Greenland, and Russia (HOLLICK 1936; KOCH 1963; BOULTER & KVAČEK 1989; AHKMETIEV 2007; BUDANTSEV & GOLOVNEVA 2009; MOISEEVA 2009, 2012; GRÍMSSON et al. 2016), and mid-latitude deposits (e.g., BROWN 1962; CHRISTOPHEL 1976; MCIVER & BASINGER 1993; DILLHOFF et al. 2005, 2013).

Pinopsida

Order Pinales

Family aff. PINACEAE

gen indet. sp. indet.

Morphotype CAF-115

Pl. 2, Fig. 3

Morphotype exemplar: YPM PB 169921-8545

Localities: YPM 8545

Description: Seed cone incomplete, 74 mm in length, 18 mm wide; base appears obtuse; apex appears acute. Cone-scale moulds appear woody, imbricate, helical; infill voids present from dispersed seeds.

Remarks: This morphotype is described from a single specimen and resembles a cone of *Pinus* L.; however, the specimen is incomplete and very little diagnostic architectural information has been preserved. Fossil macrofloral evidence of *Pinus* is not well known from the late Paleocene to early Eocene on Ellesmere and Axel Heiberg islands, but is well represented by pollen (KALKREUTH et al. 1993; MCIVER & BASINGER 1999). Nevertheless, *Pinus* pollen is known to travel great distances and so macrofloral occurrences are a better indicator of the genus' presence in the local landscape (e.g., Lowe et al. 2018). Pinaceae macrofossils become abundant in the middle Eocene Buchanan Lake deposits on Axel Heiberg (e.g. BASINGER 1991; LEPAGE & BASINGER 1991, 1995; LEPAGE 2001). These observations suggest that pinaceous conifers were present during the late Paleocene to early Eocene on Ellesmere Island, but were likely rare in the vicinity of deposition.

Order Cupressales

Family CUPRESSEACEAE

Genus cf. *Cunninghamia* R. BR.

cf. *Cunninghamia* sp.

Morphotype CAF-109

Pl. 2, Fig. 4

Morphotype exemplar: YPM PB 169858-8518

Localities: YPM 8518

Description: Leafy axis about 60 mm long, 2 mm wide; leaves acicular, arcuate, 8-11 mm long, 1-2 mm wide; phyllotaxy appears helical; apex acute to sharply acute; base sessile, weakly appressed along axis; midvein visible, occasionally prominent.

Remarks: Described from a single specimen, this fossil resembles mature foliage of *Cunninghamia* R. BR., such as specimens reported from the contemporaneous early Eocene McAbee flora of southern British Columbia by DILLHOFF et al. (2005) and LOWE et al. (2018). Fossil foliage with similar architectural characters has been previously referred to the fossil-genus *Elatides* HEER, a genus abundant in the Mesozoic and of probable affinity to Cupresseaceae (HERMAN 1994; STOCKY et al. 2005; JIN et al. 2018).

Similarities between *Cunninghamia* and *Elatides* (e.g., helical phyllotaxy, linear, lanceolate or acicular leaves, and similarity in stomatal structure and resin canals) have been recognized by others (STOCKEY et al. 2005, WANG et al. 2016; JIN et al. 2018) and suggest some overlap between the two genera. However, *Elatides* is considered to have become extinct by the Cenomanian (WANG et al. 2016; JIN et al. 2018), and use of this taxon is typically restricted to fossil foliage from the Mesozoic, whereas foliage of this type from the Cenozoic is commonly referred to *Cunninghamia*. Although this morphotype is described from a single sterile specimen, we nevertheless suggest a comparison to *Cunninghamia*; however, without accompanying fertile organs, the assignment remains tentative.

Fossils attributable to *Cunninghamia* are relatively uncommon in late Paleocene – early Eocene deposits in North America, but are well known from Late Cretaceous deposits (e.g., BRINK et al. 2009; SERBET et al. 2013; STOCKEY et al. 2018) and the Oligocene (MEYER & MANCHESTER 1997). However, some examples of *Cunninghamia* have been reported from contemporaneous mid-latitude deposits in British Columbia (STOCKEY et al. 2005; DILLHOFF et al. 2005; LOWE et al. 2018).

Genus *Metasequoia* HU et W. C. CHENG

Metasequoia occidentalis (NEWBERRY 1863) CHANEY 1951

Morphotype CAF-107

Pl. 2, Figs. 5–8

Morphotype exemplar: USPC 178-4156

Localities: USPC 6, 22, 23, 105, 108, 111, 163, 164, 175, 178, 196, 200, 251, 255, 268, 275, 367, 430, 435, 436, 438, 439, 422, 444, 657, 662, 710, 753, 1005, 1012, 1014; YPM 7936, 8432

Description: Leafy branches up to 96 mm long, oppositely branched, forming flat sprays of branchlets. Leaves opposite and decussate, rarely sub-opposite; leaves distantly spaced on branches, up to 8 mm apart along axis, closely clustered on branchlets; midvein distinct; leaf shape ovate to linear, 1.5-25 mm long, 0.5-2 mm wide; leaf apex blunt to rounded or rarely acute, base symmetrical, petiole short, attachment decurrent, attachment twisted on facial leaves. Seed cones 7-25 mm long, 7-16 mm wide, globose or ovoid, found unattached or born terminally on long bare stalks about 95 mm long; cone scale complex about 5-10 mm long, peltate, decussate. Pollen cones 2-4 mm long, 3-5 mm wide, globose, borne oppositely on stalks up to 20 mm long but incomplete. Seeds with 2 wings, flat, oval to cordate, up to 5 mm long and 4 mm wide.

Remarks: The foliar shoots and seed cones conform to the description of the genus *Metasequoia* HU et W. C. CHENG (HU & CHENG 1948; ROTHWELL & BASINGER 1979; BASINGER 1981, 1984), and to fossils referred to *Metasequoia occidentalis* (NEWBERRY) CHANEY from North America, Svalbard, and the Isle of Mull (CHANEY 1951; BROWN 1962; CHANDRASEKHARAM 1974; SCHWEITZER 1974; CHRISTOPHEL 1976; HICKEY 1977; BOULTER & KVAČEK 1989; MCIVER & BASINGER 1993; BUDANTSEV & GOLOVNEVA 2009).

Fossil specimens of *Metasequoia occidentalis* from Ellesmere Island exhibit a large degree of polymorphism, a feature observable at other fossil localities, and often held as evidence of multiple species (see LIU & BASINGER 2009). SCHWEITZER (1974) attributed foliar shoots from Svalbard with apparent alternate or sub-opposite phyllotaxy to *Parataxodium wigginsii* ARNOLD et LOWTHER, a species with similar foliar morphology to *Metasequoia* described initially from Maastrichtian deposits in Alaska (ARNOLD & LOWTHER, 1955).

BUDANTSEV& GOLOVNEVA (2009) later reassigned the Svalbard material from *Parataxodium wigginsii* to the newly established species *Metasequoia norbergii* GOLOVNEVA.

BUDANTSEV& GOLOVNEVA (2009) also recognized two additional species of *Metasequoia* from Svalbard (*M. occidentalis*, *M. distchica* (HEER) MIKI),
differentiating *Metasequoia disticha* from *M. occidentalis* based on the size of the foliage, whereas *M. norbergii* was differentiated based on size and phyllotaxy of both foliage and cones. Nevertheless, as noted by LIU & BASINGER (2009), many previous species of *Metasequoia* were established on slight morphological differences in the size and shape of foliage and cones that may represent natural morphological variation within a single species.

Although extant *Metasequoia glyptostroboides* HU et W. C. CHENG has been observed to readily produce distinct morphotypic varieties that could potentially evolve into new species (see LEPAGE et al. 2005), the available fossil evidence does not readily suggest that the morphological variance observed in the fossil assemblages is evidence of multiple species. Thus, the polymorphism observed in fossil specimens of *Metasequoia* from Ellesmere and Axel Heiberg is attributed here to morphological variety within a broad and wide-ranging natural species.

Metasequoia was a common component of many northern hemisphere plant communities throughout the early Paleogene, and has a well-documented fossil record from North America (e.g., CHANEY 1951; BROWN 1962; CHANDRASEKHARAM 1974; SCHWEITZER 1974; CHRISTOPHEL 1976; HICKEY 1977; ROTHWELL & BASINGER 1979; BASINGER 1981, 1984; MCIVER & BASINGER 1993; STOCKEY et al. 2001; LEPAGE et al. 2005), and has also been reported from Greenland, the Isle of Mull, Spitsbergen, and Northern Russia (KOCH 1964; BOULTER & KVAČEK 1989; BUDANTSEV & GOLOVNEVA 2009; MOISEEVA 2009, 2012; GRÍMSSON et al. 2016).

Genus *Glyptostrobus* ENDL.

Glyptostrobus nordenskioldii (HEER 1870) BROWN 1962

Morphotype CAF-108

Pl. 2, Figs. 9–13

Morphotype exemplar: USPC 111-4954

Localities: USPC 22, 23, 111, 444, 250, 251, 255, 259, 261, 267, 712, 753, 757, 1005, 1012, 1014; YPM 7937, 7950, 8418, 8441, 8520, 8545

Description: Branches and branchlets about 20-100 mm long; leaves polymorphic, alternate, helical, cupressoid, crypto-cupressoid, cryptomeroid, taxodioid, or crypto-taxodioid. Cupressoid leaves 1-2 mm long, appressed along stem, awl or hook shaped or straight or slightly curving, apex acute. Crypto-cupressoid leaves 1-4 mm long, may appear twisted, decurrent at base; leaves straight or curved apically. Cryptomeroid leaves 3-4 mm long, proximally straight, distally curved or hooked. Taxodioid leaves 10-20 mm long, 1-1.5 mm wide, flattened, midrib prominent, linear, apex acute, base decurrent, occasionally twisted at base. Crypto-taxodiod leaves 6-9 mm long, flattened, apices blunt to sharp. Seed cones ovate to globular, poorly preserved, open, 8-15 mm long, 5-10 mm wide; peduncles, 1-3 mm long, proximally triangular; cone scale complexes attached to a central axis, outer cone scale complex 5-9 mm long, inner cone scale complex 4-6 mm long, curving to recurved, umbo towards apex, apex acute; attached cones found primarily on crypto-cupressoid leafy branchlets; cone scales appear thin or membranous, striated, shape ovate or oblong. Pollen cones alternate and terminal, typically on branchlets that bear cupressoid leaves, globular or ovate in shape, about 2-3 mm long, about 1-2 mm wide.

Remarks: This morphotype is described from numerous specimens of sterile foliage, attached and unattached seed cones, and attached pollen cones. The fossil specimens are consistent with other material referred to *Glyptostrobus* ENDL., such as that from Svalbard (e.g., BUDANTSEV& GOLOVNEVA 2009), as well as from mid-latitude North American localities (e.g., BROWN 1962; CHRISTOPHEL 1976; HICKEY 1977; MCIVER & BASINGER 1993).

The majority of sterile foliar shoots found on Ellesmere Island are of the crypto-taxodioid leaf variety, followed by the crypto-cupressoid leaf type, the cupressoid, taxodioid, and cryptomeroid leaf types being less common within the collection (see CHRISTOPHEL 1976

for complete review of *Glyptostrobus* leaf morphology).

Following the practice of BUDANTSEV & GOLOVNEVA (2009) and others (e.g., CHANDRASEKHARAM 1974; CHRISTOPHEL 1976; MCIVER & BASINGER 1993; VIKULIN et al. 2011) this morphotype is referred to *Glyptostrobus nordenskioldii* (HEER) BROWN based on the preserved suite of architectural characters, associated reproductive material, and the strong resemblance to material previously referred to *Glyptostrobus nordenskioldii* in Canada and Svalbard.

HICKEY (1977) suggested that *Glyptostrobus europaeus* (BRONGNIART) UNGER (= *Glyptostrobus europaeus* (BRONGNIART) HEER) should be used rather than *Glyptostrobus nordenskioldii*, arguing that the morphological characters of *G. nordenskioldii* cones overlapped significantly with *G. europaeus*, and that *G. europaeus* should be applied to both the North American and European occurrences.

LEPAGE (2007) noted that many of the fossil-species established for *Glyptostrobus* were more or less identical to extant *G. pensilis* (STAUNTON ex D. DON) K. KOCH. It was also observed that many of the fossil-species of *Glyptostrobus* did not show significant differences between each other and from extant *G. pensilis*, with many of the species established based on differences in size and shape (LEPAGE 2007). Contrarily, WITTLAKE (1975) argued, based on comparisons between fossil and extant pollen cones, that significant differences exist between *G. nordenskioldii* and *G. pensilis* (see WITTLAKE 1975 for complete discussion).

Additional differences appear to exist between *G. nordenskioldii* and *G. pensilis*, and between *G. nordenskioldii* and *G. europaeus*, primarily in the number, size, and shape of seed cones and cone scale complexes (J. F. BASINGER and C. K. WEST pers. obs.). VIKULIN et al. (2011) described fossil *Glyptostrobus* remains from Ellesmere and Axel Heiberg islands as *Glyptostrobus* cf. *G. nordenskioldii*, citing differences in cone size and shape and in epidermal morphology from modern *G. pensilis*.

Furthermore, VIKULIN et al. (2011) recognized differences between *Glyptostrobus*

oregonensis Brown, a species of North American *Glyptostrobus* from the Oligocene and Miocene, and modern *G. pensilis* based on cone size and shape. These differences suggest that there continues to be a need to differentiate between Paleogene populations of *Glyptostrobus* and Neogene populations of *Glyptostrobus* pending further taxonomic review of *Glyptostrobus* species.

Glyptostrobus was a common floral element during the early Paleogene in North America and Europe, in both high- to mid-latitude localities, as well as Greenland, Spitsbergen, the Isle of Mull, and Northern Russia (e.g. HEER 1878a, 1882; NEWBERRY 1898; KNOWLTON 1930; HOLLICK 1936; BROWN 1936, 1962; CHANDRASEKHARAM 1974; SCHWEITZER 1974; CHRISTOPHEL 1976; HICKEY 1977; BOULTER & KVAČEK 1989; MCIVER & BASINGER 1993; LEPAGE 2007; BUDANTSEV & GOLOVNEVA 2009; MOISEEVA 2009, 2012).

Genus *Elatocladus* HALLE

Elatocladus cordillera CHRISTOPHEL 1976

Morphotype CAF-111

Pl. 2, Fig. 14

Morphotype exemplar: USPC 436-2742

Localities: USPC 436; YPM 8432

Description: Incomplete foliar shoots; leaves alternate, helical, taxodioid to crypto-taxodioid; leaf shape lanceolate, ovate, or linear; leaves 5-35 mm long, 1.5-2 mm wide; apices rarely preserved, but appear rounded or blunt when preserved; leaf base decurrent, petiolate, attached obliquely to axis.

Remarks: This morphotype is described from several incomplete sterile foliar shoots that resemble material from the Smoky Tower locality of Alberta and the Ravenscrag Formation of Saskatchewan (CHRISTOPHEL 1976; MCIVER & BASINGER 1993). This morphotype only exhibits the taxodioid leaves described by CHRISTOPHEL (1976).

The alternate and helical phyllotaxy differentiates this morphotype from branches and

branchlets referred to *Metasequoia occidentalis*, which displays an opposite, decussate phyllotaxy. Neither do the architectural elements of this morphotype conform to the morphological features of *Glyptostrobus* foliage, which are typically much smaller in size.

The fossil-species *Elatocladus cordillera* CHRISTOPHEL was established by CHRISTOPHEL (1976) for foliar remains that resembled extant genera (e.g., *Metasequoia*, *Sequoia* ENDL., *Taxodium* RICHARD, and *Glyptostrobus*) that CHRISTOPHEL considered either too few in number or incomplete to determine a reasonable generic identification.

CHRISTOPHEL (1976) noted that although this species was artificial, it could be used to avoid potential palaeoecological and phytogeographical errors caused by assigning taxodiaceous Cupresseaceae foliar remains, based on either limited specimens or poorly preserved fossils, to extant taxa. Thus, this morphotype is referred to the fossil-species *Elatocladus cordillera* until additional material with sufficient morphological characteristics or associated reproductive organs are found.

A diversity of foliar remains referred to *Elatocladus* HALLE and similar taxodiaceous Cupresseaceae fossil foliage are well known throughout the fossil record in North America during the early Paleogene, and have been reported from both high- and mid-latitudes (e.g., HEER 1868; NEWBERRY 1898; HOLLICK 1936; BROWN 1962; CHANDRASEKHARAM 1974; CHRISTOPHEL 1976; MCIVER & BASINGER 1993). Fossils referred to *Elatocladus* have also been reported from Spitsbergen and Northern Russia (BUDANTSEV & GOLOVNEVA 2009; MOISEEVA 2009, 2012).

Genus *Thuja* L.

Thuja polaris MCIVER et BASINGER 1989a

Morphotype CAF-135

Pl. 3, Figs. 1–2

Morphotype exemplar: USPC 101-3393

Localities: USPC 101

Description from MCIVER & BASINGER (1989a, p. 2-4): "Branching alternate, irregular, forming flattened sprays; branches moderately divided, pinnatelike; branchlets slender; distinctly flattened, rarely overlapping, arising in the axils of lateral branch leaves, about 5.0-7.0 mm apart, well separated on axis, becoming more crowded at apex. Leaves scale-like, decussate, persistent; facial leaves appressed, resin glands rarely present on branch leaves, not present or inconspicuous on branchlet leaves; lateral leaves folded along midrib; branch and branchlet leaves dissimilar. Facial leaves of branchlets ovate to very wide obovate, 1.0-2.0 mm long, 1.0-2.1 mm wide; apex acute to acuminate. Lateral leaves of branches 1.0-2.0 mm long, 0.5-2.0 mm wide, partially overlapping succeeding facial leaf; apex acute to obtuse, rarely free; juncture of lateral leaves concealed by preceding facial leave. Facial leaves of branches linear to oblong, 2.0-6.0 mm long, 1.5-1.8 mm wide; apex acute to obtuse, thickened. Lateral leaves of branches linear or falcate, 2.0-6.0 mm long, 0.5-1.2 mm wide, partially overlapping succeeding facial leaf; apex acute, free; juncture of lateral leaves concealed by preceding facial leaf. Seed cones oblong or elliptic, about 10.0 mm long and 6.0 mm wide, bearing 8-9 decussate pairs of scales; cones terminating reflexed, leafy axis. Cone scales oblong to ovoid, 1.5-6.0 mm long, up to 4.0 mm wide, 0.3-0.4 mm thick; scales thin, leathery, bearing distinct reflexed umbo on the apophysis; basal pair of scales about 1.5 mm long; apical pair rudimentary and forming a columella-like structure about 2.0 mm long. Pollen cones and seeds not known".

Remarks: The fossil-species *Thuja polaris* MCIVER et BASINGER was established for fossil foliage with attached cones from Ellesmere Island (see MCIVER & BASINGER 1989a, for complete discussion on *Thuja polaris*). The fossil is characterized by alternately branching foliage with distinct flattened branchlets, and small scale-like decussate leaves that are persistent along the branch axis. The seed cones are typically ovate or obovate, or rarely oblong, in shape with 8-9 pairs of oblong to ovoid cone scales (MCIVER & BASINGER 1989a).

Early Paleogene vegetative remains referred to *Thuja* L. have been well documented from North America (e.g., NEWBERRY 1868, 1895; LESQUEREUX 1883; BROWN 1962; HICKEY

1977; DILLHOFF et al. 2005), and have also been reported from Alaska, Greenland, Svalbard, and the Canadian Arctic (e.g., HEER 1870, 1874, 1882; HOLLICK 1936; MCIVER & BASINGER 1989a; BUDANTSEV & GOLOVNEVA 2009). It is noted below that *Cupressinocladus* sp. 2 bears resemblance to *T. polaris*, and indeed could represent additional occurrences. Nevertheless, without attached, or at least associated cones it is not possible to confirm assignment of cupressaceous foliage from other localities to *Thuja polaris*, and therefore occurrence of *T. polaris* is recognized only at the type locality.

Genus *Cupressinocladus* SEWARD (nom. cons.)

Cupressinocladus sp. 1

Morphotype CAF-121

Pl. 3, Figs. 5 & 12

Morphotype exemplar: YPM PB 169897-7937

Localities: YPM 7937

Description: Branch incomplete, branching alternate, forming flat sprays, up to 160 mm long; branchlets narrow, arising at junctions of lateral leaves, about 11-36 mm long, about 5-10 mm apart along axis; branchlets bear crowded, opposite, ultimate branchlets. Leaves scale-like, decussate, persistent, lanceolate to ovate to obovate, may appear striated. Facial leaves of branches 2-3 mm long, about 0.5 mm wide, appressed; base appears decurrent; apex rounded or blunt; lateral leaves of branches rarely preserved or obscured by branchlets, 2-3 mm long, < 0.5 mm wide, lanceolate. Facial leaves of branchlets 1-3 mm long, about 0.5 mm wide; base appears decurrent but typically obscured by preceding lateral leaves; apex rounded to blunt or rarely acute. Lateral leaves of branchlets 1.5-2 mm long, about 0.5 mm wide, falcate; base appears narrow or decurrent; apex acute, typically obscured or expressed at wide angles resulting from branchlets. Facial leaves of ultimate branchlets about 1 mm long, about 0.5 mm wide, appressed, appear obovate; base obscured by preceding lateral leaves; apex acute or blunt. Lateral leaves of ultimate branchlets 1-1.5 mm long, ≤ 0.5 mm wide, falcate or hooked,

typically appressed.

Remarks: This morphotype is described from a single specimen of a sterile shoot that consists of part and counterpart. The alternately branching flat sprays and typically appressed decussate scale-like leaves are consistent with Cupressaceae. This morphotype is differentiated from *Cupressinocladus* sp. 2 (e.g., morphotype CAF-136, see below) as the branchlets bear crowded, opposite, ultimate branchlets. This morphotype is differentiated from *Thuja polaris*, as *T. polaris* was described from both foliar shoots and cones (McIver & Basinger 1989a), and does not demonstrate the habit of crowded ultimate branchlets.

As no fertile material was found in association with this specimen, it is assigned to the noncommittal fossil-genus *Cupressinocladus* Seward, a name conserved by Zijlstra & Kvaček (2010). This implies a connection to Cupressaceae, but refrains from associating the morphotype with a potentially spurious assignment to either an extant genus or a previously established fossil-genus (e.g. *Thuja polaris* or *Mesocyparis borealis* McIver et Basinger).

Specimens of *Thuja* and *Thuja*-like fossils are well documented from early Paleogene localities in North America at both mid- and high-latitudes (e.g., Newberry 1868, 1898; Berry 1935; Hollick 1936; Bell 1949; Brown 1962; Christophel 1976; Hickey 1977; McIver & Basinger 1993), and from Greenland, and Svalbard (e.g., Heer 1870, 1874, 1882; Schweitzer, 1974; Budantsev & Golovneva 2009); however, many of these assignments are either doubtful or should be transferred to *Cupressinocladus* (see McIver & Basinger 1989a).

Cupressinocladus sp. 2

Morphotype CAF-136

Pl. 3, Figs. 6 & 8

Morphotype exemplar: USPC 753-2129

Localities: USPC 102, 251, 753

Description: Branches incomplete, appear alternate or opposite, forming flat sprays, up to 85

mm long; branchlets narrow, arising at junctions of lateral leaves, up to 25 mm long, about 10 mm apart along axis; branchlets may bear ultimate branchlets that appear alternate, or opposite, or may appear upon one side of branchlet only. Leaves scale-like, decussate, persistent. Facial leaves of branches poorly preserved or obscured by lateral leaves, and rarely observed, 1-3 mm long, ≤ 0.5 mm wide, appressed; apex rounded or blunt. Lateral leaves of branches about 1-2 mm long, < 0.5 mm wide, lanceolate, may be expressed at wide angles resulting from junctions of branchlets. Facial leaves of branchlets 0.5-1.5 mm long, ≤ 1 mm wide, typically obscured by preceding lateral leaves or poorly preserved, appear obovate, appressed; apex round to rarely acute. Lateral leaves of branchlets 2-3 mm long, about 0.5-1 mm wide, falcate or lorate; base appears rounded; apex rounded or blunted to rarely apiculate. Facial leaves of ultimate branchlets, typically obscured almost completely by preceding lateral leaves, when visible about 1 mm long, about 0.5-1 mm wide, shape appears elliptic; apex rounded. Lateral leaves of ultimate branchlets 1-1.5 mm long, ≤ 1 mm wide, appear elliptic or falcate, typically appressed; base appears rounded; apex round to rarely acute. Associated seed cone poorly preserved, incomplete, not attached; 1 or 2 cone scale complexes excurrently attached to a central axis; cone scale complex about 0.5 mm long, 1-3 mm wide; central axis about 1-1.5 mm long.

Remarks: This morphotype is described from multiple incomplete specimens. Similar to CAF-121, the flat sprays and appressed, decussate, scale-like leaves are consistent with sterile shoots attributable to Cupressaceae. This morphotype is differentiated from *Cupressinocladus* sp. 1 (i.e., CAF-121) as the facial leaves of the branchlets and ultimate branchlets of that morphotype are typically well exposed and easily observed, whereas the facial leaves of this morphotype are often obscured by the overlapping lateral leaves and are harder to observe.

This morphotype is differentiated from *Thuja polaris* as that taxon was based on both foliage and cones, whereas this morphotype is based primarily on sterile foliar shoots. The associated seed cone, although poorly preserved, does appear to resemble a cupressaceous cone, but was unattached. Furthermore, the branching pattern of *Thuja polaris* is described as

alternate, where the branching pattern of this morphotype appears to be inconsistently either opposite or alternate. This feature may be the result of damage or preservation quality but remains a significant variation from the established diagnosis of *Thuja polaris*.

As previously noted with CAF-121, various fossil forms of *Thuja* and *Cuppressinocladus* fossils have been reported from early Paleogene fossil localities in North America, Greenland, and Svalbard (see above).

Order *Incertae sedis*

Family *INCERTAE SEDIS*

gen. indet. sp. indet.

Morphotype CAF-085

Pl. 3, Fig. 3

Morphotype exemplar: YPM PB 169824-8432

Localities: YPM 8432

Description: Leaf poorly preserved, about 3.5 cm long but incomplete, about 1-1.3 cm wide at widest point; apex not preserved; base angle acute, base shape round. Margin untoothed. Primary venation straight, strongly parallel, 12-14 veins. Higher order venation not observed.

Remarks: This morphotype is described from a single specimen that preserves three incomplete leaflet fragments. This morphotype is distinguished by strong parallel primary venation and untoothed margins. The limited material prevents a reliable systematic assignment; however, in handwritten notes that accompanied this specimen, L. J. HICKEY indicated that these specimens were potentially cycad leaflets. This taxonomic association would seem speculative given the limited information preserved on the fossil.

gen. indet. sp. indet.

Morphotype CAF-148

Pl. 3, Fig. 4

Morphotype exemplar: USPC 261-6326

Localities: USPC 261

Description: Apparent leafy branchlet, incomplete, 10 mm long, 1 mm wide, bearing leaves apparently helically arranged; leaves ovate, appear sessile, leaves robustly keeled abaxially, about 2 mm long, 1 mm wide; apex acute; branchlet appears to bear a terminal leaf.

Remarks: This morphotype is described from a single specimen and may represent an as-yet unknown conifer. The leaves are prominently keeled abaxially, an architectural character not apparent in other fossil conifer foliage found in the Canadian palaeoarctic.

gen. indet. sp. indet.

Morphotype CAF-152

Pl. 3, Fig. 7

Morphotype exemplar: USPC 166-4267

Localities: USPC 166

Description: Apparent leaflets, incomplete, about 30 mm long, 28 mm wide, appear ovate. Margin appears untoothed. Primary venation parallel. Rachis stout, about 4 mm wide, 65 mm long but incomplete.

Remarks: This morphotype is described from a single specimen that preserves three incomplete leaflet fragments. This morphotype is notable for the strong parallel primary venation and untoothed margins of the apparent leaflets and a robust rachis. The specimen superficially resembles fossil cycads (e.g., HOLLICK 1932; ERDEI et al. 2012). The limited material precludes a reliable systematic assignment.

gen. indet. sp. indet.

Morphotype CAF-139

Pl. 3, Figs. 9–10

Morphotype exemplar: USPC 23-1270

Localities: USPC 23

Description: Cone scale 9-12 mm long, shape obovate, 7-10 mm wide distally, 2-3 mm wide proximally; proximal portion appears dark and woody; distal edge appears entire, may also appear chewed or toothed, possibly the result of damage; prickle not observed.

Remarks: These cone scales are larger than others observed from Ellesmere Island and appear to be coniferous; however, these cone scales were not found in association with fossil foliage.

MAGNOLIOPSIDA

Magnoliids

Order Magnoliales

Family aff. MAGNOLIACEAE

Genus cf. *Magnolia* L.

cf. *Magnolia* sp.

Morphotype CAF-102

Text-fig. 3.9, Pl. 3, Fig. 11

Morphotype exemplar: USPC 111-4885

Localities: USPC 111, 163, 261

Description: Leaf notophyllous, elliptic, symmetrical, length-to-width ratio about 2:1, petiolate; attachment marginal; apex shape straight, apex angle acute; base shape convex, base angle acute. Leaf margin untoothed. Primary venation pinnate, with 1 basal vein; agrophic veins absent. Major secondary venation brochidodromous; secondary vein spacing irregular, secondary vein angle uniform; attachment to midvein proximally decurrent and distally excurrent; inter-secondary veins absent. Tertiary venation mixed opposite-alternate percurrent; tertiary vein angle obtuse to midvein, tertiary vein course convex.

Remarks: This morphotype was described from two specimens and is defined by its elliptic shape, entire margin, and brochidodromous secondary venation. The secondary and tertiary

venation is well preserved and suggests that the leaf may have been coriaceous. Architectural characteristics suggest this leaf may have been a type of *Magnolia* L.

Similar fossils from Svalbard were referred to *Magnoliaephyllum* SEWARD by BUDANTSEV & GOLOVNEVA (2009), and the Ellesmere Island fossils closely resemble a fragmentary specimen referred to as *Magnoliaephyllum* sp. 1 (BUDANTSEV & GOLOVNEVA 2009, p. 363, pl. 78, fig. 1-3). The Ellesmere Island specimens are well preserved and nearly complete, and many of the foliar characters are reminiscent of extant *Magnolia*, and the specimens also resemble fossils referred to *Magnolia magnifolia* KNOWLTON by BROWN (1962). Nevertheless, as noted by MANCHESTER (2014) the foliar characteristics common to *Magnolia* foliage (i.e., entire margins and pinnate venation) are neither unique to nor diagnostic of *Magnolia.*

Nevertheless, affinity to the Magnoliaceae and comparison to the genus *Magnolia* is suggested, but without the accompaniment of supporting fertile organs, the assignment remains tentative. Various early Paleogene leaf fossils have been referred to as *Magnolia* or *Magnolia*-like in North America, Europe, Russia and the polar latitudes (e.g., NEWBERRY 1898; HOLLICK 1936; BROWN 1962; AHKMETIEV 2007; BUDANTSEV & GOLOVNEVA 2009).

Monocots

Order Zingiberales

Family ZINGIBERACEAE

Genus *Zingiberopsis* HICKEY

Zingiberopsis cf. *Z. isonervosa* HICKEY 1977

Morphotype CAF-118

Pl. 3, Fig. 13

Morphotype exemplar: USPC 100-6260

Localities: USPC 6, 100, 105

Description: Leaves fragmentary and incomplete, mesophyllous or larger. Leaf untoothed. Costa robust, about 6 mm at widest point. Major secondary veins parallel, numerous, spaced ≤ 0.5 mm apart. Secondary veins diverge from midrib at acute angles about 20-25°. Tertiary veins when visible are thin, straight, evenly spaced, and tightly packed; tertiary vein angle obtuse or nearly perpendicular to midrib; tertiary veins form cross-connections to adjacent secondary veins; tertiary vein course straight or convex.

Remarks: Fossil material assigned to this morphotype is fragmentary and incomplete; however, characteristics are present that are shared by similar fossil material referred to *Zingiberopsis* HICKEY (1977). Shared characteristics include: a robust midrib; closely spaced secondaries composed of a single vein order that diverge from the midrib at acute angles; and, tertiary veins that form connections between adjacent secondary veins (HICKEY 1977). The tertiary veins of the Ellesmere Island material are typically poorly preserved, although some specimens show tertiary venation similar to *Zingiberopsis isonervosa* HICKEY *sensu* HICKEY & PETERSON (1978).

Musopsis groenlandicum BOYD, a fossil-species similar to *Zingiberopsis,* is readily differentiated by the obtuse angle at which the secondary venation diverges from the midrib (BOYD 1992). Morphotype CAF-118 was described from three fragmentary specimens; however, enough characters are present to suggest a possible relationship to *Zingiberopsis isonervosa*.

Large monocotyledonous fossils aligned, in some cases dubiously, with Zingiberaceae or other families within the Zingiberales from the early Paleogene are well documented from the mid- to high-latitudes (e.g., HEER 1869, 1874; LESQUEREUX 1878; BROWN 1962; HICKEY 1977; HICKEY & PETERSON 1978; BOYD 1990, 1992; MOISEEVA et al. 2018).

Order *Incertae sedis*

Family *INCERTAE SEDIS*

gen. indet. sp. indet.

Morphotype CAF-096

Pl. 4, Fig. 2

Morphotype exemplar: YPM PB 169875-8545

Localities: YPM 8545

Description: Leaf fragment incomplete, about 16 mm long, 7 mm wide. Primary venation forms parallel sets; sets composed of two coarse parallel primary veins bracketing finer gauge parallel primary veins. Secondary venation forms even sets of transverse veins that cross the preceding primary longitudinal veins; secondary veins are uniform, rarely offset; secondary vein course convex or straight.

Remarks: This morphotype was described from a single incomplete specimen. Fossil fragments with similar vein patterns were reported from the Golden Valley Formation of the Williston Basin in North Dakota by HICKEY (1977, pl. 11, fig. 2, 3), who noted that fossils with similar venation patterns have previously been referred to the extant genus *Typha* L. However, HICKEY (1977) also notes that similar vein patterns can be found in many genera of aquatic or semi-aquatic monocots, and that this particular vein architecture should not be used as the sole criterion for taxonomic assignment. Thus, taxonomic assignment for this morphotype is precluded.

gen. indet. sp. indet.

Morphotype CAF-133

Pl. 4, Figs. 1 & 3

Morphotype exemplar: USPC 437-2782

Localities: USPC 436, 437

Description: Leaf fragmented, costa robust, about 7-9 mm wide. Major secondary venation parallel to midrib before diverging nearly orthogonally; secondary veins numerous, irregularly spaced, appear to be ranked into multiple.

Remarks: This morphotype is described from two fragmented specimens that preserve only a

portion of the lamina interior. The secondary venation is complex and appears to be composed of sets of veins of differing thickness that run parallel to the midrib before diverging at, or nearly at, orthogonal angles. These are characters shared by fossil specimens from Greenland referred to *Musopsis groenlandicum* by BOYD (1992); however, the preservation of the Ellesmere Island specimens is poor, which makes it impossible to ascertain if the necessary pattern of secondary veins is present as observed in *M. groenlandicum.*

The width of the costa in the Ellesmere Island specimen is much narrower than that illustrated by BOYD (1992) (i.e., < 1.5 cm), although this may be a result of the preserved portion representing a distal region of the leaf, or possibly an immature leaf. This morphotype is easily differentiated from superficially similar fossils such as *Zingiberopsis*, as the parallel sets of secondary veins diverge from the costa at orthogonal angles, whereas the secondary vein sets of *Zingiberopsis* diverge from the costa at acute angles.

The preserved architectural characters suggest these specimens share some affinity with *Musopsis* BOYD; however, as only poorly preserved fragments are available, the taxonomic assignment is precluded.

Fossil leaves similar to this morphotype have been previously reported from Greenland (e.g., BOYD 1990, 1992), and superficially similar leaves (e.g., *Musophyllum complicatum* LESQUEREUX) have been reported from the mid to high-latitudes (e.g., LESQEUREUX 1878; BROWN 1962; HICKEY 1977).

Eudicots

Order Proteales

Family NELUMBONACEAE

Genus cf. *Nelumbo* ADANS.

cf. *Nelumbo* sp.

Morphotype CAF-072

Pl. 4, Figs. 4–5

Morphotype exemplar: YPM PB 169879-8546

Localities: YPM 7950, 8410, 8417, 848, 8545, 8546

Description: Two fragmentary leaves, orbicular, appearing centrally peltate. Primary venation actinodromous, with 16-26, prominent, straight, unbranching basal veins that extend radially from a prominent central disc.

Remarks: This morphotype was described from two poorly preserved specimens, but reported by L. J HICKEY from a total of six localities. HICKEY& WOLFE (1975) described leaves of Nelumbonaceae as simple, peltate, untoothed, and actinodromous with multiple primary veins. Although the two specimens recovered from Ellesmere Island are fragmentary, many of these characters are observed, which suggests an assignment to Nelumbonaceae is justified.

The taxonomic affinity of *Nelumbo*-like fossils can be narrowed down based on the architecture of the margin. For example, the fossil genera *Nelumbites* BERRY, *Paleonelumbo* KNOWLTON, and *Exnelumbites* ESTRADA-RUIZ, UPCHURCH, WOLFE, et CEVALLOS-FERRIZ are characterized by some form of dentition along the margin (HE et al. 2010; ESTRADA-RUIZ et al. 2011), whereas the fossil-genus *Nelumbago* MCIVER et BASINGER and the extant genus *Nelumbo* ADANS. are characterized by an untoothed margin (HICKEY & WOLFE 1975; MCIVER & BASINGER 1993).

In addition, the higher order venation may be used to further refine the taxonomic affinity of *Nelumbo*-like specimens. For example, quadrangular areolation is diagnostic of *Nelumbago montanum* (BROWN) MCIVER et BASINGER, whereas hexagonal areolation is diagnostic of both fossil and extant *Nelumbo* (HICKEY 1977; MCIVER & BASINGER 1993; HE et al. 2010).

Unfortunately, the Ellesmere Island specimens do not have any margin or higher order tertiary veins preserved. Despite lacking these architectural characters, the presence of a central disc—a character distinct to *Nelumbo*—suggests this morphotype is aligned to the extant genus

Nelumbo (ESTRADA-RUIZ et al. 2011); however, as the morphotype is based on a small number of fragmented and incomplete specimens, the specific assignment remains uncertain.

Fossil specimens assigned to *Nelumbo* and *Nelumbo*-like genera are common in many contemporaneous mid-latitude fossil localities (e.g., BROWN 1962; HICKEY 1977; MCIVER & BASINGER 1993). No *Nelumbo* or *Nelumbo*-like fossils have been described from Svalbard, Greenland, or the sub-Arctic Isle of Mull (HEER 1868; BOULTER & KVAČEK 1989; BUDANTSEV & GOLOVNEVA 2009), although fragmentary fossils from Alaska were referred to *Nelumbo protolutea* BERRY by HOLLICK (1936).

Family PLATANACEAE

Genus *Macginitiea* WOLFE et WEHR

Macginitiea aff. *M. nobilis* (NEWBERRY 1868) MANCHESTER 2014

Morphotype CAF-080

Text-fig. 3.10, Pl. 4, Figs. 6–8, Pl. 5, Figs. 1–2, 4

Morphotype exemplar: YPM PB 169818-8547

Localities: US 168, 367, 1005, 1012; YPM 7950, 8439, 8413, 8418, 848, 8545, 8547

Description: Leaf mesophyllous, petiolate, attachment marginal, obovate to ovate, palmately lobed, length-to-width ratio about 1-1.5:1, symmetrical; apex shape straight, apex angle acute; base shape concave to truncate, base angle obtuse. Leaf margin untoothed to rarely slightly erose with rare irregular teeth. Primary venation basal palinactinodromous, with 3 basal veins; simple agrophic veins present. Major secondary venation brochidodromous; interior secondary veins present, merging to form chevrons between primary veins; secondary vein spacing irregular; secondary vein angle uniform; attachment to midvein excurrent; inter-secondary veins weakly present. Tertiary venation opposite; tertiary vein angle obtuse to midvein, tertiary vein course straight.

Remarks: This morphotype has characteristic palinactinodromous primary venation and interconnected secondary veins between adjacent primary veins that form chevrons, which

distinguishes it as the genus *Macginitiea* WOLFE et WEHR (MANCHESTER 1986; WOLFE & WEHR 1987; MANCHESTER 2014).

The Ellesmere Island *Macginitiea* resembles fossils referred to *Macginitiea nobilis* (NEWBERRY) MANCHESTER (NEWBERRY 1898; HICKEY 1977; PIGG & STOCKY 1991; MANCHESTER 2014). Similar to *Macginitiea nobilis,* the Ellesmere Island *Macginitiea* is 3-lobed, whereas *Macginitiea gracilis* (LESQUEREUX) WOLFE et WEHR is commonly 5-lobed (MANCHESTER 2014). CAF-080 has three primary lobes that are shallowly incised, and two small basal toothy projections, similar to a specimen of *Macginitiea nobilis* figured by MANCHESTER (2014, p. 12, fig. 5.2).

This Ellesmere Island *Macginitiea* is described from a limited number of specimens, most either fragmented or incomplete. Although the available evidence indicates that the assignment to the genus *Macginitiea* is appropriate, the limited material available for description and study suggests the assignment to *Macginitiea nobilis* should remain tentative.

Macginitiea is known from multiple early Paleogene mid-latitude localities from North America (e.g., BROWN 1962; HICKEY 1977; MANCHESTER 1986; WOLFE & WEHR 1987; PIGG & STOCKEY 1991). HOLLICK (1936) reported from a single locality a limited record of *Macginitiea nobilis* (= *Platanus nobilis* NEWBERRY) in Alaska. *Macginitiea* has not been recorded from Greenland, Spitsbergen, or the Isle of Mull.

Genus *Macginicarpa* MANCHESTER

Macginicarpa cf. *M. manchesteri* PIGG et STOCKEY 1991

Morphotype CAF-126

Pl. 5, Fig. 3

Morphotype exemplar: YPM PB 169907-8433

Localities: YPM 8422

Description: Inflorescence unattached, dispersed, globose, about 20 mm in diameter; appears to

contain achenes, achenes appear elliptical, about 6 mm long, 2-3 mm wide, apparent persistent styles up to 3 mm long, styles appear curved, present in groups of three, four, or five, but specimens are damaged and incomplete.

Remarks: This morphotype resembles fossils recovered from contemporaneous sediments from mid-latitudes in North America (e.g., MANCHESTER 1986; PIGG & STOCKEY 1991), and resembles compression specimens recovered from the late Paleocene of Alberta referred to *Macginicarpa manchesteri* PIGG et STOCKEY (1991).

This morphotype was described from several incomplete specimens from a single locality and was not found in association with any fossil leaves referable to *Macginitiea*. As such the taxonomic affinity of this morphotype remains tentative.

Genus *Platanus* L.

Platanus sp.

Morphotype CAF-128

Text-fig. 3.11, Pl. 5, Figs. 5–6, 10

Morphotype exemplar: USPC 111-4879

Localities: USPC 111, 367

Description: Leaf notophyllous to mesophyllous, petiolate, attachment marginal, ovate, length-to-width ratio about 1-1.5:1, appears basally asymmetrical; apex shape appears straight but is incomplete, apex angle obtuse; base shape cordate to lobate, base angle reflexed. Leaf margin appears toothed but is damaged or incomplete. Primary venation basal palinactinodromous, with 3 basal veins; simple agrophic veins present. Major secondary venation appears craspedodromous; secondary vein spacing gradually increases proximally; secondary vein angle uniform; attachment to midvein excurrent; inter-secondary veins absent. Tertiary venation opposite percurrent; tertiary vein angle obtuse to midvein; tertiary vein course straight to convex.

Remarks: The basal palinactinodromous venation suggests this morphotype belongs to the

Platanaceae. This morphotype does not have interior secondary veins that meet between adjacent primaries to form chevrons, and as such is not referable to *Macginitiea* (i.e., CAF-080). Morphotype CAF-128 resembles fossils from Svalbard that were referred to *Platanus basicordata* BUDANTSEV (BUDANTSEV & GOLOVNEVA 2009), but differ in that the Ellesmere Island specimens have deeply lobed bases and do not appear to be trilobed, as is typical of this species; however, the specimens available are fragmented and incomplete and the small lobes observed in *P. basicordata* may not have been preserved in the Ellesmere Island fossils.

Platanaceous leaves are common floral elements of mid to high latitude floras from the Paleogene in the Northern Hemisphere (CRANE 1989; MANCHESTER 1986; UPCHURCH & WOLFE 1987), and are considered to be highly polymorphic (UPCHURCH 1984; BOULTER & KVAČEK 1989; BUDANTSEV & GOLOVNEVA 2009).

Order Trochodendrales

Family TROCHODENDRACEAE

Genus *Nordenskioeldia* HEER

Nordenskioeldia borealis HEER 1870

Morphotype CAF-112

Pl. 5, Figs. 7–9

Morphotype exemplar: USPC 261-6334

Localities: USPC 111, 261, 435

Description: Infructescence bearing fruits; fruits pedunculate, sessile, 5-7 mm long, 5-6 mm wide, appear ovoid or globose, born in groups of two, three, or possibly four; peduncle up to 54 mm long, 1 mm wide, but incomplete; internodal space between fruits 10-12 mm; fruits are divided into smaller fruitlets, up to 16 fruitlets observed but many incomplete, fruitlets whorled around a central column. Dispersed fruitlets not observed.

Remarks: This morphotype resembles fossil material previously referred to *Nordenskioeldia*

borealis HEER and to *Nordenskioeldia* HEER as described by CRANE et al. (1991) and BUDANTSEV & GOLOVNEVA (2009). The size and shape of the follicles make unattached specimens easily differentiated from *Nyssidium arcticum*, a racemose fossil infructescence also found on Ellesmere Island.

CRANE et al. (1991) showed that *Nordenskioeldia* is aligned with the Trochodendraceae, although this relationship has been challenged and is in need of further study (e.g., DOWELD 1998; MANCHESTER et al. 2018). The *Nordenskioeldia* morphotype may be related to the *Tetracentron* sp. morphotype (e.g., CAF-040), but as these two morphotypes were not found in association with one another in the Ellesmere collection, their potential relationship remains unresolved.

Nordenskioeldia has been reported from both mid- and high- latitudes in North America, Svalbard, Greenland, and Russia (e.g., HEER 1868, 1870; HOLLICK 1936; KOCH 1963; CHANDRASEKHARAM 1974; KVAČEK et al. 1994; CRANE et al. 1991; BUDANTSEV & GOLOVNEVA 2009; GRÍMSSON et al. 2016; MOISEEVA et al. 2018).

Genus *Tetracentron* OLIV.

Tetracentron cf. *T. hopkinsii* PIGG, DILLHOFF, DEVORE et WEHR 2007

Morphotype CAF-040

Text-fig. 3.12

Morphotype exemplar: USPC 422-3871

Localities: USPC 22, 422

Description: Leaf mesophyllous, petiolate, attachment marginal, elliptic, length-to-width ratio about 1.5:1, symmetrical; apex shape acuminate, apex angle acute; base shape cordate, base angle reflexed. Leaf margin serrately crenate, with 1 order of teeth, 3 teeth/cm, regularly spaced, shape convex/convex, sinus angular, tooth apex appears glandular. Primary venation basal actinodromous, with 5 basal veins; simple agrophic veins present. Major secondary venation festooned semicraspedodromous; secondary vein spacing uniform; secondary vein angle and

spacing uniform; inter-secondary veins absent. Tertiary venation opposite percurrent; tertiary vein angle obtuse to midvein; tertiary vein course straight to sinuous.

Remarks: This morphotype is consistent with the fossil-species *Tetracentron hopkinsii* PIGG, DILLHOFF, DEVORE et WEHR described by PIGG et al. (2007) in general shape, cordate base, and acute to acuminate apex. CAF-040 also displays the same venation architecture, such as the thin midrib with two or three pairs of lateral primaries. The leaf margin in these forms is serrate with very regular rounded teeth along all but the basal-most margins of the cordate lobes, also like *T. hopkinsii*.

The shape and of number teeth per centimeter characteristic to this morphotype are also similar to *T. hopkinsii* (PIGG et al. 2007). Furthermore, a large single vein centrally feeds the teeth, but these veins are further connected by a pair of smaller veins that reach towards the sinuses of the neighboring teeth, a characteristic diagnostic of the genus *Tetracentron* OLIV., and distinguishing it from morphotypes with similar marginal dentition (i.e., morphotype CAF-021, *Trochodendroides crenulata* KVAČEK, MANUM et BOULTER) (WOLFE 1977; PIGG et al. 2007).

This morphotype is described from limited fossil material, which precludes a firm taxonomic assignment at this time. Fossils assigned to *Tetracentron* have been identified from Alaska, British Columbia, and Washington (WOLFE 1977; PIGG et al. 2007), as well as Russia (e.g., AHKMETIEV 2007), but are not reported from Svalbard or the Isle of Mull.

Core Eudicots

Order Saxifragales

Family CERCIDIPHYLLACEAE

Genus *Archeampelos* MCIVER et BASINGER

Archeampelos cf. *A. acerifolia* (NEWBERRY 1868) MCIVER et BASINGER 1993

Morphotype CAF-034

Text-fig. 3.13, Pl. 6, Figs. 1–2

Morphotype exemplar: USPC 436-2732.2

Localities: USPC 6, 436, 167,169, 173, 174, 178, 179, 196, 200, 261, 1005, 1012

Description: Leaf notophyllous to mesophyllous, elliptic, tri-lobed, petiolate, attachment marginal, length-to-width ratio about 1-1.5:1, symmetrical; apex shape convex, apex angle acute; base shape truncate to weakly cordate, base angle obtuse. Leaf margin serrately to dentately crenate, with 1 order of teeth, 1 tooth/cm, regular spacing, shape convex/convex, sinus rounded or angular, tooth apex glandular or retuse. Primary venation actinodromous, with 5-7 basal veins; simple agrophic veins present. Major secondary venation craspedodromous, secondary vein spacing decreasing apically, secondary vein angle uniform, attachment to midvein excurrent; inter-secondary veins strongly present. Tertiary venation alternate percurrent, tertiary vein angle obtuse to midvein, tertiary vein course convex.

Remarks: These fossils strongly resemble material reported from Russia, Svalbard, Alaska, and the mid-latitudes of North America (e.g., NEWBERRY 1868; HOLLICK 1936; BELL 1949; BROWN 1962; CHANDRASEKHARAM 1974; MCIVER & BASINGER 1993; BUDANTSEV & GOLOVNEVA 2009; PEPPE 2009; MOISEEVA et al. 2018), which have been previously identified as *Acer arcticum* HEER (e.g., HEER 1876; HOLLICK 1936; BELL 1949; BUDANTSEV & GOLOVNEVA 2009) or as *Archeampelos acerifolia* (NEWBERRY) MCIVER et BASINGER (= *Populus acerifolia* NEWBERRY = *Ampelopsis acerifolia* (NEWBERRY) BROWN) (e.g., NEWBERRY 1868; BROWN 1962; CHANDRASEKHARAM 1974; MCIVER & BASINGER 1993; PEPPE 2009).

The Ellesmere Island material aligns closely with the *Archeampelos* MCIVER et BASINGER diagnosis of MCIVER & BASINGER (1993), and the *A. acerifolia* description and diagnostic characteristics (i.e., large distinctive teeth and a rounded to truncate base) provided by PEPPE (2009).

PEPPE (2009) noted that *Archeampelos* should not be placed in the Vitaceae because of specific architectural characters (e.g., primary and secondary venation, distinctive tooth

morphology), and that it more likely belongs within the Cercidiphyllaceae. MANCHESTER (2014), in his revision of BROWN's (1962) flora, supported assignment of *Archeampelos* to the Cercidiphyllaceae based on foliar characteristics and the presence of marginal glands.

Previous studies have suggested that the material identified as both *Acer arcticum* and *Archeampelos acerifolia* should be combined into a single genus (WOLFE & TANAI 1987). WOLFE & TANAI (1987) described the *Acer arcticum* complex as likely representing an extinct genus of *Acer* L. based on a combination of characters not found in extant species of *Acer.*

BUDANTSEV& GOLOVNEVA (2009) in their review of fossil material from Svalbard, assigned leaves similar to morphotype CAF-034 to *Acer arcticum*; however, they suggested that the Svalbard material could not be assigned to *Archeampelos* based on dental characteristics and the angle at which the primary basal veins diverged from the midvein (BUDANTSEV & GOLOVNEVA 2009). The Svalbard material has basal veins that diverge from the midvein at wide angles, up to 50-60°, angles wider than is typical for leaves referred to *Archeampelos* from mid-latitude localities (BUDANTSEV & GOLOVNEVA 2009). Additionally, BUDANTSEV & GOLOVNEVA (2009) noted that forms assigned to *Archeampelos acerifolia* may have acute teeth, a character never observed in *Acer arcticum*. However, both the emended diagnosis of *Archeampelos acerifolia* from MCIVER & BASINGER (1993) and the diagnostic characters provided by PEPPE (2009) describe *Archeampelos acerifolia* as having only large round teeth.

Although the Ellesmere Island fossil material strongly resembles the Svalbard material assigned to *Acer arcticum* in architectural character, including the laminar dentition and the wide angle of divergence of basal primary veins (approximately 40-50°), the fossils found on Ellesmere Island commonly have glandular teeth (pl. 6, fig. 2), which precludes them from being assigned to *Acer*. It is possible that the retuse or emarginate teeth commonly observed in specimens assigned to *Acer arcticum* from other polar and mid-latitude localities may be the result of missing glands, the glands having been lost or torn out as is common in members of the Cercidiphyllaceae (PIGG et al. 2007).

It is worth noting that the morphological suit of characteristics of morphotype CAF-034 do not align exactly with the existing species concept of *Archeampelos acerifolia* and therefore it is likely a variant unique to the Canadian Arctic.

Genus *Nyssidium* HEER

Nyssidium arcticum (HEER 1869) ILJINSKAJA 1974

Morphotype CAF-088

Pl. 6, Figs. 5–6

Morphotype exemplar: USPC 261-6335

Localities: USPC 111, 165, 169, 251, 261, 367, 371, 430; YPM 8415

Description: Infructescence pedunculate, peduncle up to 58 mm long, 2-3 mm wide, bearing follicles. Follicles helical but may appear alternate when compressed, pedicellate, borne in pairs or solitary, found attached or unattached, elliptic to ovate, appear flattened, 8-26 mm long, 2-8 mm wide; apex rounded or acute; base rounded or acute; pedicel 1-2.5 mm long, 0.5-1.5 mm wide. Follicles with up to 10 parallel external longitudinal striations, with internal striations at right angles to external striations; follicles dehisce abaxially along a longitudinal suture. Some specimens may preserve remnants of seeds.

Remarks: This morphotype is described from multiple specimens and is consistent with material previously referred to *Nyssidium arcticum* (HEER) ILJINSKAJA, such as that from the late Paleocene Ravenscrag Formation in Saskatchewan, Canada (MCIVER & BASINGER 1993), as well as material from Svalbard (BUDANTSEV & GOLOVNEVA 2009).

This morphotype also resembles the Cercidiphyllaceous inflorescence of *Joffrea speirsii* CRANE et STOCKEY from the late Paleocene in Alberta, Canada (CRANE & STOCKEY 1986). Although the two species closely resemble each other, the fruits differ in a single architectural element. The fruits of *Nyssidium arcticum* from Ravenscrag dehisce along an abaxially oriented ventral suture, whereas *Joffrea speirsii* always dehisces adaxially (CRANE & STOCKEY 1985;

MCIVER & BASINGER 1993). Abaxial dehiscence is observed in *Nyssidium* HEER from Ellesmere Island, which indicates that this morphotype represents *Nyssidium arcticum*, rather than *Joffrea speirsii*.

BUDANTSEV& GOLOVNEVA (2009) distinguished between *Nyssidium arcticum* and *Nyssidium ekmanii* HEER, where *N. ekmanii* was used for smaller dispersed solitary fruits as originally described by HEER (1870) from Spitsbergen, and *N. arcticum* for fruits connected to a racemose stem.

Nyssidium was originally established by HEER (1870) for five new species of fruit from Spitsbergen (i.e., *Nyssidium ekmanii*, *N. crissum* HEER, *N. oblongum* HEER, *N. lanceolatum* HEER, and *N. fusiforme* HEER), which were later combined into a single species, *Nyssidium ekmanii*, by ILJINSKAJA (1974). *Nyssa arctica* HEER was first described from the Paleocene of West Greenland by HEER (1869), and was later transferred to *Nyssidium* by ILJINSKAJA (1974) to form *Nyssidium arcticum. Nyssidium arcticum* and *N. ekmanii* were differentiated by ILJINSKAJA (1974) based on size and shape of the follicles.

CRANE (1984), in his review of similar infructescences and fruits from England, considered *N. arcticum* and *N. ekmanii* to be conspecific, with *N. arcticum* taking nomenclatural priority. This concept of *Nyssidium arcticum* has come to be used for many fossils of similar construction (GOLOVNEVA & ALEKSEEV 2017).

Recently, GOLOVNEVA & ALEKSEEV (2017) have proposed that *Nyssidium* should be replaced by the fossil-genus *Jenkinsella* REID et CHANDLER, arguing that no evidence exists that *N. ekmanii*, as described by HEER (1870), had a racemose fruit arrangement or winged seeds, and that the similarity between "*Nyssa*" *arctica* and *Nyssidium ekmanii* appears superficial.

They further argue that *Nyssidium ekmanii* has too few distinctive architectural characters and as a result could accommodate many systematically different taxa (GOLOVNEVA & ALEKSEEV 2017). Nevertheless, this argument would seem in conflict with their own findings, as they state that, based on their reexamination of fossil material, the general

construction of these fruits and infructescences are practically identical and that the minor differences observed are not sufficient for generic designation.

CRANE (1984) came to a similar conclusion and noted that many of the established *Nyssidium* taxa may very well be synonymous, as few satisfactory qualitative characters appear to exist to convincingly differentiate between *N. arcticum* and other *Nyssidium* species. As a result, CRANE (1984) intentionally provided no specific diagnosis for his concept of *Nyssidium arcticum*. Thus, the argument to substitute *Nyssidium*, a well-established and widely used fossil-genus, by *Jenkinsella* would seem inappropriate.

Following CRANE (1984), both solitary fruits and those found connected to an infructescence from Ellesmere and Axel Heiberg islands are referred to *Nyssidium arcticum*, as the morphology for the follicles, whether connected or solitary, appears to be identical.

It has been shown that plants that produced fruits of this type were either cercidiphyllaceous or possibly related to extant *Cercidiphyllum* (CRANE 1984; CRANE & STOCKEY 1985). Thus, these infructescences and fruits may be produced by the same plants that produce *Trochodendroides* leaves common to Ellesmere Island.

Fruits of this type have been reported from both high- and mid-latitude localities from the early Paleogene from North America, Svalbard, Greenland, and Russia (e.g., HOLLICK 1936; BROWN 1939 and references therein; CRANE 1984; MCIVER & BASINGER 1993; BUDANTSEV & GOLOVNEVA 2009; MOISEEVA 2009, 2012; MOISEEVA et al. 2018).

Genus *Trochodendroides* BERRY 1922

Remarks: The complex of leaves of the *Trochodendroides* BERRY type was a common element of many early Paleogene fossil localities from the Arctic to the mid-latitudes (e.g., HEER 1868; NEWBERRY 1898; BERRY 1926; HOLLICK 1936; SCHLOEMER-JÄGER 1958; BROWN 1962; CHANDRASEKHARAM 1974; CHRISTOPHEL 1976; HICKEY 1977; BOULTER & KVAČEK 1989; MCIVER & BASINGER 1993; BUDANTSEV & GOLOVNEVA 2009). These leaves are extremely

polymorphic, resulting in the problematic description of many taxa.

The generic affinity of these troublesome fossils has also proved to be a challenge, many authors having regarded them as ancestral to the modern *Cercidiphyllum* SIEBOLD et ZUCC. (e.g., BROWN 1939, 1962; CHANDRASEKHARAM 1974; HICKEY 1977), while others prefer to avoid associating these fossil leaves with a modern genus and prefer the fossil-genus *Trochodendroides* (e.g., BERRY 1926; CRANE 1984; KVAČEK & BOULTER 1989; BUDANTSEV & GOLOVNEVA 2009; MANCHESTER 2014)—a practice followed herein. The polymorphism shown in the proposed modern relatives (e.g., *Cercidiphyllum japonicum* SIEBOLD & ZUCC. ex J. J. HOFFM. & J. H. SCHULT. bis), as reviewed by CHANDRASEKHARAM (1974), within a single tree among short shoot, long shoot, and sucker shoot leaves, suggests that the extent of splitting in the literature is artificial, increasing the number of taxa and compromising the utility of a flora as a palaeoenvironmental proxy.

Leaves attributed to *Trochodendroides* are typically basally acrodromous with festooned semicraspedodromous secondary venation, with rounded apices and truncate, rounded, or cordate bases. The marginal teeth of *Trochodendroides* leaves may sometimes preserve glands; however, when glands are not present it may be because they are either missing, pulled out, or destroyed, likely due to taphonomic processes (PIGG et al. 2007).

Fossils of this type described by HEER (1868) were placed in *Populus* L. as *P. richardsonii* HEER, *P. arctica* HEER, and *P. zaddachii* HEER. Similar fossil leaves from North American floras were described by NEWBERRY (1863, 1898), also as *Populus* (e.g., *P. elliptica* NEWBERRY, *P. cordata* NEWBERRY, *P. genetrix* NEWBERRY, and many others), and as other genera (e.g., *Piper* L., *Paliurus* MILL., *Ziziphus* MILL., *Grewia* L., *Cercis* L., *Ficus* L.) by other authors (e.g., WARD 1886; LESQUEREUX 1878; NEWBERRY 1898; KNOWLTON 1899; HOLLICK 1936). BERRY (1926) encountered leaves similar to HEER'S polar *Populus* concept in Paleogene floras from British Columbia, but rejected the association to *Populus*, and created the combination *Trochodendroides arctica* (HEER) BERRY, using the previously established fossil-

genus *Trochodendroides* (BERRY 1922).

BROWN (1939) recognized that the confusion inherent in leaves of this type resulted in unintentional conflation of taxa and the unnecessary creation of additional taxa. BROWN (1939) then attributed these fossil forms to the modern genus *Cercidiphyllum* and established four different *Cercidiphyllum* species (e.g., *Cercidiphyllum ellipticum* (NEWBERRY) BROWN, *Cercidiphyllum arcticum* (HEER) BROWN, *Cercidiphyllum elongatum* BROWN, *Cercidiphyllum crenatum* (UNGER) BROWN). *Cercidiphyllum arcticum,* a new combination by BROWN that used HEER'S (1866) basionym *Populus arctica*, combined fifty other additional taxa (see BROWN 1939 for complete *Cercidiphyllum arcticum* synonomy).

WOLFE (1966) later recognized three major types in BROWN'S concept of *Cericidphyllum arcticum*, and established *Trochodendroides serrulata* (WARD) WOLFE, *Cocculus flabella* (NEWBERRY) WOLFE, and *Dicotylophyllum richardsonii* (HEER) WOLFE. HICKEY (1977) would take this concept further and established the "*Cercidiphyllum arcticum* complex" of the Fort Union and Golden Valley formations. HICKEY (1977) noted that the holotype of BROWN'S (1939) basionym for *C. arcticum* had been synonymized with "*Cocculus" flabella* (i.e., WOLFE 1968), and thus the earliest described form that could be referred to this species was *Populus genetrix* NEWBERRY, and is given priority over the specific epithet of '*flabella*'. HICKEY (1977) placed quotations around "*Cocculus"* as he felt the assignment was suspect, but refrained from referring it to a new genus.

The "*Cercidiphyllum arcticum* complex" as described by HICKEY (1977) included five different taxa (i.e., *Cericidphyllum genetrix* (NEWBERRY) HICKEY*, "Cocculus" flabella, Trochodendroides serrulata, Dicotylophyllum richardsonii,* and *Dicotylophyllum mercerensis* HICKEY). MANCHESTER (2014) recombined *Cercidiphyllum genetrix, Trochodendroides serrulata,* and many other forms treated by BROWN (1962) and others (e.g., BROWN 1939; HICKEY 1977) into *Trochodendroides genetrix* (NEWBERRY) MANCHESTER, noting that as the leaves of *Trochodendroides genetrix* did not match the lectotype for *Trochodendroides arctica*

(= *Populus arctica* = *Cercidiphyllum arcticum*) from Greenland, then *T. genetrix* represents a separate leaf complex from North America.

BUDANTSEV& GOLOVNEVA (2009), in their extensive review of the early Paleogene Svalbard fossil flora, provided taxonomic revision to previously established Spitsbergen forms (e.g., SCHLOEMER-JÄGER 1958), preferring the fossil-genus *Trochodendroides,* citing the complexities still remaining in assigning fossil leaves to a modern genus.

BUDANTSEV & GOLOVNEVA (2009) recognized seven *Trochodendroides* species (*Trochodendroides arctica, Trochodendroides retusa* BUDANTSEV et GOLOVNEVA, *Trochodendroides richardsonii* (HEER) KRYSHTOFOVICH, *Trochodendroides nathorstii* (BUDANTSEV) GOLOVNEVA, *Trochodendroides heerii* (BUDANTSEV) GOLOVNEVA, *Trochodendroides crenulata*, and *Trochodendroides curvidens* (HEER) GOLOVNEVA et BUDANTSEV) based on a suite of variable leaf architectures that commonly displayed some degree of morphological overlap. Certain characters used, such as a tendency to better preserve secondary or higher order venation, were used to further delineate between species, but these characters may have resulted from preservational bias and may not reflect actual taxonomic separation.

Trochodendroides morphotypes in this study are grouped using laminar dentition, as laminar dentition more effectively sorted *Trochodendroides*-type leaves from Ellesmere and Axel Heiberg islands into fewer distinct morphotypes. As a result; however, of using primarily laminar dentition to group *Trochodendroides*-type leaves, some of the Svalbard *Trochodendroides* taxa described by BUDANTSEV & GOLOVNEVA (2009) are considered here to informally represent the same species. The morphotypes described from Ellesmere and Axel Heiberg islands are considered here to represent four distinct taxa: *Trochodendroides arctica, T. curvidens, T. crenulata,* and *T. richardsonii*.

Trochodendroides arctica (HEER 1868) BERRY 1926

Morphotype CAF-035

Text-fig 3.14, Pl. 6, Figs. 3–4, Pl. 7, Fig. 1

Morphotype exemplar: USPC 439-2809.2

Localities: USPC 6, 22, 105, 108, 111, 251, 255, 163, 166, 168, 169, 170, 173, 196, 200, 261, 439, 444

Description: Leaf microphyllous to notophyllous, petiolate, attachment marginal, ovate to orbicular to rarely elliptic or reniform, length-to-width ratio about 1.5:1, symmetrical; apex shape straight to convex to rounded, apex angle obtuse to rarely acute; base shape cordate, base angle obtuse to reflexed. Leaf margin erose to untoothed to notched to occasionally irregularly toothed with serrate crenulations. Primary venation acrodromous, with 3 to 7 (5) basal veins; simple agrophic veins present. Major secondary venation festooned brochidodromous to festooned semicraspedodromous; secondary vein spacing uniform; secondary vein angle uniform; attachment to midvein excurrent; inter-secondary veins absent. Tertiary venation mixed opposite-alternate percurrent; tertiary vein angle obtuse to perpendicular to midvein.

Remarks: There is considerable morphological overlap between *Trochodendroides arctica* and certain forms of *Trochodendroides* found on Ellesmere and Axel Heiberg islands. BUDANTSEV & GOLOVNEVA (2009) described *Trochodendroides arctica* as typically having an erose, irregularly toothed, or entire margin; rarely this form may also display marginal notches or irregular teeth that are serrately crenate. Many of these traits are shared by *Trochodendroides retusa* (BUDANTSEV & GOLOVNEVA 2009), which is noted as being more commonly entire margined and never displaying marginal notches or irregular teeth. Additionally, *T. arctica* and *T. retusa* were separated by BUDANTSEV & GOLOVNEVA (2009) because the tertiary vein preservation of *T. retusa* commonly displayed greater relief than that of leaves assigned to *T. arctica*. As these architectural traits share significant overlap, or may be related to differences in preservation, we consider *T. arctica* to include *T. retusa* for this study.

Many fossil specimens of this type from the mid-latitudes of North America, Alaska, Greenland, the Isle of Mull, Spitsbergen, and Russia have been previously referred to

Trochodendroides (HOLLICK 1936; BROWN 1939, 1962; KOCH 1964; CHANDRASEKHARAM 1974; HICKEY 1977; BOULTER & KVAČEK 1989; AHKMETIEV 2007; BUDANTSEV & GOLOVNEVA 2009; MOISEEVA 2009, 2012; GRÍMSSON et al. 2016; MOISEEVA et al. 2018).

Trochodendroides curvidens (HEER 1876) GOLOVNEVA et BUDANTSEV 2009

Morphotype CAF-036

Text-fig. 3.15, Pl. 7, Fig. 4

Morphotype exemplar: USPC 436-2750

Localities: USPC 6, 22, 111, 163, 166, 200, 436

Description: Leaf microphyllous to notophyllous, petiolate, attachment marginal, ovate to elliptic, length-to-width ratio about 1:1, symmetrical; apex shape acuminate, apex angle acute; base shape cordate, base angle reflexed. Leaf margin finely to coarsely serrate, with 1 order of teeth, 4 teeth/cm, regularly spaced, shape convex/straight to convex/concave, sinus rounded, apex simple. Primary venation acrodromous, with 3-7 (5) basal veins; simple agrophic veins present. Major secondary venation festooned semicraspedodromous; secondary vein spacing uniform; secondary vein angle uniform; attachment to midvein is excurrent; inter-secondary veins absent. Tertiary venation mixed opposite-alternate percurrent; tertiary vein angle obtuse to perpendicular to midvein.

Remarks: This is the only *Trochodendroides* morphotype from the Canadian palaeoarctic that has sharply acute teeth. This morphotype resembles similar fossil material described from Svalbard by BUDANTSEV & GOLOVNEVA (2009) and referred to the species *Trochodendroides curvidens*; their interpretation is followed here.

Trochodendroides crenulata (HEER 1876) KVAČEK, MANUM et BOULTER 1994

Morphotype CAF-021

Text-fig. 3.16, Pl. 7, Figs. 2 & 5

Morphotype exemplar: USPC 435-2706.1

Localities: USPC 6, 22, 105, 108, 111, 163, 169, 172,175, 196, 200, 251, 435, 442

Description: Leaf microphyllous to mesophyllous, petiolate, attachment marginal, elliptic to orbicular to ovate to rarely reniform, length-to-width ratio about 1:1 to 0.75:1, symmetrical; apex shape rounded to rarely straight to rarely convex, apex angle obtuse to rarely acute; base shape truncate to rarely convex to rarely cordate, base angle obtuse to reflexed. Leaf serrately crenate to rarely dentately crenate, with 1 order of teeth, 3-5 teeth/cm, regularly spacing, shape convex/convex to convex/concave to convex/retroflexed to retroflexed/retroflexed to retroflexed/convex, sinus rounded, apex simple or glandular. Primary venation basal acrodromous to rarely suprabasal acrodromous, with 3-7 (5) basal veins; simple agrophic veins present. Major secondary venation festooned semicraspedodromous; secondary vein spacing increasing proximally; secondary vein angle increases proximally; attachment to midvein excurrent; inter-secondary veins absent. Tertiary venation opposite percurrent; tertiary vein angle obtuse to midvein; tertiary vein course straight to sinuous.

Remarks: This morphotype resembles fossils assigned to *Trochodendroides heerii* and *Trochodendroides crenulata* (herein considered to be the same taxon) described from Svalbard by BUDANTSEV & GOLOVNEVA (2009). Both taxa possess numerous small rounded well-ordered teeth; however, the teeth of *T. heerii* commonly form longer teeth with deeper sinuses, whereas the teeth of *T. crenulata* are typically shorter with shallower sinuses, and *T. crenulata* is also noted for commonly having better-preserved venation.

The overlap in tooth morphology of these two taxa, however, is continuous, which suggests that they represent variation within a single species. The marginal dentition of morphotype CAF-021 is regular, serrately crenate, and varies between longer and shorter forms of dentition; teeth are rarely glandular, the glands being rarely preserved, or are missing, pulled out, or destroyed, likely due to taphonomic processes (PIGG et al. 2007).

We retain the name *Trochodendroides crenulata* for our assignment, as the basionym for *T. crenulata* was established as *Grewia crenulata* HEER (1876), whereas *Trochodendroides*

heerii (= *Cercidiphyllum heerii* BUDANTSEV) was established much later by BUDANTSEV (1983).

Trochodendroides richardsonii (HEER 1868) KRYSHTOFOVICH 1958

Morphotype CAF-098

Text-fig. 3.17, Pl. 7, Figs. 3 & 6

Morphotype exemplar: USPC 435-2696

Localities: USPC 22, 105, 111, 163, 169, 170, 173, 175, 179, 196, 200, 261, 435,

Description: Leaf notophyllous to mesophyllous, petiolate, attachment marginal, ovate to rarely orbicular to rarely reniform, length-to-width ratio about 0.5-0.75:1 to 1:1, symmetrical; apex shape rounded to straight, apex angle obtuse; base shape truncate to cordate, base angle obtuse to reflexed. Leaf margin serrately crenate, with 1 order of teeth, 1-1.5 teeth/cm, shape convex/convex to convex/retroflexed, regularly spaced, sinuses angular to rounded, simple to rarely glandular apices. Primary venation basal acrodromous, with 3-5 (7) basal veins; simple agrophic veins present. Major secondary venation festooned semicraspedodromous; secondary vein spacing increases proximally; secondary vein angle increasing proximally; attachment to midvein excurrent; inter-secondary veins absent. Tertiary venation mixed opposite percurrent; tertiary vein angle obtuse to midvein.

Remarks: This morphotype shares multiple morphological characteristics with other fossil forms assigned to the genus *Trochodendroides*; however, CAF-098 is easily recognizable by the large, broad teeth, which are commonly rounded but may occasionally present as broadly deltoid (i.e., pl. 7 fig. 3).

This morphotype is similar to the species *Trochodendroides richardsonii*, described from Svalbard as having large broad, rounded, regularly spaced teeth (BUDANTSEV & GOLOVNEVA 2009). *Trochodendroides richardsonii* resembles *Trochodendroides nathorstii*, also described from Svalbard but considered a separate taxon, as *T. nathorstii* commonly has large, broad, triangular teeth (BUDANTSEV & GOLOVNEVA 2009). For the purpose of this study,

however, we consider *T. richardsonii* and *T. nathorstii* to be the same, as these foliar characteristics may simply represent variation within a single taxon.

Gen indet. sp. indet.

Morphotype CAF-144

Pl. 7, Figs. 7–8

Morphotype exemplar: USPC 200-4756

Localities: USPC 111, 200

Description: Possible bracts or seeds, shape triangular, 3-4 mm long, 1-3 mm wide; apex acute, apex shape straight; base obtuse, base shape truncate or rounded or rarely chevron-shaped; may appear darkened along margins.

Remarks: These fossils may represent seeds or possibly bracts and do appear similar to bracts belonging to the staminate inflorescences of *Joffrea speirsii* from the late Paleocene Joffre Bridge locality in Alberta, Canada (CRANE & STOCKEY 1984); however, the taxonomic affinity remains unresolved as these fossils were not found in association with any fossil foliage.

Rosids

Order Vitales

Family aff. VITACEAE

Genus *Vitiphyllum* NATHORST

Vitiphyllum cf. *V. sewardii* BOULTER et KVAČEK 1989

Morphotype CAF-004

Text-fig. 3.18, Pl. 7, Figs. 9–10

Morphotype exemplar: USPC 442-2820

Localities: USPC 173, 174, 178, 179, 196, 200, 261, 275, 367, 422, 432, 434, 436, 442, 657, 712, 1005, 1012, 1014

Description: Leaf notophyllous to mesophyllous, petiolate, attachment marginal, ovate, length-

to-width ratio about 0.75-1:1, symmetrical to weakly asymmetrical; apex shape convex, apex angle acute; base shape cordate, base angle reflexed. Leaf margin dentate to serrate, with 2 order of teeth, 5 teeth/cm, regularly spaced, shape convex/straight to convex/concave to straight/concave, sinus angular, apex simple. Primary venation basal actinodromous, with 5 basal veins; compound agrophic veins present. Major secondary venation craspedodromous; secondary vein spacing regular; secondary vein angle uniform; attachment to midvein excurrent to weakly decurrent; inter-secondary veins absent. Tertiary venation opposite percurrent; tertiary vein angle obtuse to midvein; tertiary vein course convex.

Remarks: This morphotype strongly resembles fossils from the Isle of Mull referred to as *Vitiphyllum sewardii* BOULTER et KVAČEK. Similar architectural characters include the preponderance of generally very large lamina, deeply lobed cordate bases, strong agrophic veins, a pair of basal veins that branch from the midrib at nearly right angles, and tertiary veins that form an alternating series of meshes.

Superficially, the size and shape of these fossils can appear similar to forms of *Platanus* L. or *Platanites* FORBES from the Paleocene of North America; however, morphotype CAF-004 is easily distinguished from platanoid material as the primary venation is never palinactinodromous, and no fewer than 5 basal veins are ever observed radiating from a central point. This morphotype is easily separated from the Ellesmere Island fossils referred to *Archeampelos* (i.e., CAF-034), as the basal cordate lobes of *Vitiphyllum* NATHORST are much larger and deeply incised, and the leaves of *Archeampelos* from Ellesmere Island are all coarsely toothed with large, broad, round, glandular teeth.

Vitiphyllum sewardii from the Isle of Mull was described from specimens that exhibit a blunt round-toothed margin (BOULTER & KVAČEK 1989), whereas the specimens from Ellesmere Island may also occasionally display some smaller serrated teeth that are either acute or crenate, in addition to the more typical blunted tooth margins observed in the Ardtun specimens. Fossil leaves similar to *Vitiphyllum* from both Ellesmere Island and the Isle of Mull

have been found on Spitsbergen, but were referred to *Acer thulense* HEER (BOULTER & KVAČEK 1989; BUDANTSEV & GOLOVNEVA 2009).

In the absence of fossil seeds, fruits, or other organs, the taxonomic assignment follows the cautious approach recommended by BOULTER & KVAČEK (1989), and the fossil-genus *Vitiphyllum* is used rather than the extant genus *Vitis* L. Furthermore, as the Ellesmere Island *Vitiphyllum* fossils do not adhere exactly to the diagnosis of *Vitiphyllum sewardii*, the taxonomic assignment ultimately remains tentative.

Fossil leaves referred to either *Vitiphyllum* or *Vitis* have been found in other early Paleogene fossil localities in North America, the Isle of Mull, Greenland, and potentially from Spitsbergen (HEER 1869; KOCH 1963; CHANDRASEKHARAM 1974; BOULTER & KVAČEK 1989; BUDANTSEV & GOLOVNEVA 2009; GRÍMSSON et al. 2016).

Fabids

Order Fagales

Family BETULACEAE

Genus *Alnus* MILL.

Alnus cf. *A. parvifolia* (BERRY 1926) WOLFE et WEHR 1987

Morphotype CAF-061

Text-fig. 3.19, Pl. 8, Fig. 1

Morphotype exemplar: USPC 267-6353

Localities: USPC 259, 267, 268, 753

Description: Leaf notophyllous, petiolate, attachment marginal, ovate, length-to-width ratio about 1.5:1, symmetrical; apex shape straight, apex angle obtuse; base shape round, base angle obtuse. Leaf margin serrate, with 2 orders of teeth, 3-4 teeth/cm, regularly spaced, shape convex/straight to straight/retroflexed, sinus rounded, apex simple. Primary venation pinnate,

with 1 basal vein; agrophic veins absent. Major secondary venation craspedodromous; secondary vein spacing regular; secondary vein angle uniform; attachment to midvein weakly decurrent. Tertiary venation opposite percurrent; tertiary vein angle obtuse to midvein; tertiary vein course straight to sinuous.

Remarks: This morphotype resembles the species *Alnus parvifolia* (BERRY) WOLFE et WEHR, a fossil-species of *Alnus* MILL. typically found in contemporaneous localities in southern British Columbia and Washington (WOLFE & WEHR 1987; DILLHOFF et al. 2005). Shared architectural characters include: the elliptical to ovate leaf shape; the obtuse to decurrent base shape; acute to acuminate apices a serrate margin with 3-5 subsidiary teeth between each primary tooth; and, teeth that are convex to straight on the distal flank.

This morphotype also shares some similarity with *Alnus inaequale* (HEER) BUDANTSEV et GOLOVNEVA, a species described from Spitsbergen; however, *A. inaequale* typically has more pairs of major secondary veins (11-14) and sharper teeth than the Ellesmere Island form (see BUDANTSEV & GOLOVNEVA 2009).

Woody infructescences also referred to *Alnus* (i.e., CAF-091, see below) have been recovered from Ellesmere Island, but were not found in association with fossil *Alnus* leaves; therefore, the foliage and reproductive material have not been treated as a single morphotype.

Alnus was abundant throughout the early Cenozoic of the Northern Hemisphere and has been documented from multiple localities across North America, Europe, Russia, Asia, and the Arctic (e.g., HOLLICK 1936; BROWN 1962; WOLFE 1977; CRANE 1981; WOLFE & WEHR 1987; AHKMETIEV 2007; BUDANTSEV & GOLOVNEVA 2009; LIU et al. 2014).

Alnus sp.

Morphotype CAF-091

Pl. 8, Figs. 2–3, 8

Morphotype exemplar: USPC 275-6138

Localities: USPC 261, 275, 422, 1014

Description: Mature infructescence, found singly or rarely as branched pairs, ellipsoid or weakly globose, about 10-25 mm long, 8-14 mm wide; 11-23 bract scales appear helically arranged around a central axis; bracts thick; wedge- or hook-shaped.

Remarks: This morphotype resembles infructescences previously referred to *Alnus* (e.g., HOLLICK 1936; WOLFE & WEHR 1987; DILLHOFF et al. 2005), and have been reported previously from the Canadian Arctic from middle Eocene deposits on Axel Heiberg Island (BASINGER 1991).

Although these infructescences resemble material from Republic (Washington, USA) referred to as *Alnus parvifolia* by WOLFE & WEHR (1987), these infructescences were not found attached or in association to any fossil leaves referable to *Alnus.* Furthermore, WOLFE & WEHR (1987) did not provide a description of the infructescences they figured, which prevents detailed comparison. Thus, until additional material is recovered for analysis, the specific affinity of these *Alnus* infructescences remains unresolved.

Genus cf. *Paracarpinus* MANCHESTER et CRANE

cf. *Paracarpinus* sp.

Morphotype CAF-031

Text-fig. 3.20, Pl. 8, Figs. 6–7

Morphotype exemplar: USPC 22-1143

Localities: USPC 22, 435; YPM 8423

Description: Leaf notophyllous, petiolate, attachment marginal, elliptic, length-to-width ratio about 2:1, symmetrical; apex angle acute, apex shape straight; base angle obtuse, base shape rounded to weakly cordate. Leaf margin serrate, with 1 order of teeth, 4 teeth/cm, regularly spaced, shape convex/concave to retroflexed/convex to straight/convex, sinus angular, apex simple. Primary venation pinnate, with 3 basal veins; simple agrophic veins present. Major secondary venation craspedodromous; secondary vein spacing gradually increasing proximally;

secondary vein angle uniform; attachment to midvein decurrent; inter-secondary veins absent. Tertiary venation opposite percurrent; tertiary vein angle obtuse to midvein; tertiary vein course straight to convex.

Remarks: This morphotype is similar to the fossil-genus *Paracarpinus* MANCHESTER et CRANE (1987), a genus erected to accommodate fossil material with characteristics of modern *Carpinus* L., but without attributed reproductive material. The Ellesmere Island fossils also resemble fossil material referred to *Craspedodromophyllum* CRANE, a fossil-genus erected for leaves found in association with the extinct fruit *Palaeocarpinus* CRANE (1981).

Although *Paracarpinus* and *Craspedodromophyllum* share morphological characters common to foliage aligned with Betulaceae (e.g., serrate margins, craspedodromous venation, parallel secondary veins), they differ primarily in that leaves of *Craspedodromophyllum* have a cuneate base, whereas leaves belonging to *Paracarpinus* typically have a rounded or cordate base—a feature also typical of this Ellesmere morphotype.

It is important to note that the Spitsbergen form of *Craspedodromophyllum,* a type also recognized in the Ellesmere Island fossil flora (see morphotype CAF-051 below), does have a cordate base; however, the Spitsbergen *Craspedodromophyllum* is typified by a much wider lamina than the leaves that were used to establish the genus by CRANE (1981).

The Ellesmere Island material also shares some architectural similarities with *Carpinus nathorstii* BUDANTSEV, a fossil taxon described from Spitsbergen (BUDANTSEV & GOLOVNEVA 2009). *Carpinus nathorstii* has an evenly serrate margin, straight to gently arcuate secondary venation that curves apically, and rounded or cordate bases (BUDANTSEV & GOLOVNEVA 2009), architectural characters similar to the Ellesmere Island morphotype. However, as this morphotype is described from limited fragmentary material, and with no supporting reproductive material recovered from Ellesmere Island, an assignment to the modern genus *Carpinus* is inadvisable. Thus, this morphotype is tentatively referred to the fossil-genus *Paracarpinus.*

Carpinus and *Paracarpinus* have been described from Alaska, Svalbard, North America, and Asia (e.g., HOLLICK 1936; TANAI 1972; CRANE 1981; BUDANTSEV & GOLOVNEVA 2009), but are considered uncommon elements in North American vegetation until the Neogene or Quaternary (MANCHESTER 1999).

Genus *Corylites* GARDNER ex SEWARD et HOLTTUM

Corylites hebridicus SEWARD et HOLTTUM 1924

Morphotype CAF-129

Text-fig. 3.21, Pl. 8, Figs. 4–5, 9

Morphotype exemplar: USPC 367-3896

Localities: USPC 22, 23, 111, 200, 250, 251, 255, 261, 367, 369, 371

Description: Leaf mesophyllous, petiolate, attachment marginal, ovate to elliptic, length-to-width ratio about 1.5-2:1, symmetrical; apex shape straight, apex angle acute; base shape weakly to strongly cordate, base angle reflexed. Leaf margin dentately crenate, with 1 to 2 orders of teeth, 2-4 teeth/cm, regularly spaced, shape is convex/convex to convex/retroflexed to retroflexed/convex to straight/convex, sinus angular, apex simple. Primary venation pinnate, with 3 basal veins; compound agrophic veins present. Major secondary venation craspedodromous; secondary vein spacing gradually increasing proximally; secondary vein angle uniform; attachment to midvein decurrent and a uniform vein angle; inter-secondary veins absent. Tertiary venation opposite percurrent; tertiary vein angle obtuse to midvein; tertiary vein course convex.

Remarks: This morphotype strongly resembles fossil foliage referred to *Corylites hebridicus* SEWARD et HOLTTUM, reported from the Ardtun flora of the Isle of Mull and from Svalbard (SEWARD & HOLTTUM 1924; BOULTER & KVAČEK 1989; BUDANTSEV & GOLOVNEVA 2009). Shared architectural elements include: the ovate shape; cordate bases; typically straight to gently curved parallel secondary veins; basal secondary veins that open from the midvein orthogonally

or at much lower angles than the more distal secondary veins; and, robust deltoid-shaped teeth.

The strong similarity and shared architectural characteristics support assignment of the Ellesmere Island specimens to *Corylites hebridicus*. The fossil-genus *Corylites* GARDNER ex SEWARD et HOLTTUM is used, as no associated reproductive material has been recovered from Ellesmere Island that would support assignment to extant *Corylus* L.

Various fossil forms of *Corylus*-like and *Corylites* foliage are well known from many Paleocene and Eocene localities across the Arctic, North America, Europe, Spitsbergen, the Isle of Mull, and Northern Russian (NEWBERRY 1898; HOLLICK 1936; BROWN 1962; HICKEY 1977; BOULTER & KVAČEK 1989; SUN & STOCKEY 1992; MANCHESTER 1999; BUDANTSEV & GOLOVNEVA 2009; MOISEEVA 2009, 2012).

Genus *Craspedodromophyllum* CRANE

Craspedodromophyllum cf. *C. malmgrenii* (HEER 1868) GOLOVNEVA 2002

Morphotype CAF-054

Text-fig. 3.22, Pl. 8, Fig. 10, Pl. 9, Fig. 1

Morphotype exemplar: USPC 200-4777

Localities: USPC 111, 200, 444, 1012

Description: Leaf notophyllous, petiolate, attachment marginal, ovate, length-to-width ratio about 1.5:1, symmetrical; apex angle acute, apex shape straight; base angle obtuse to reflexed, base shape cordate to rounded. Leaf margin serrate to dentate, with 1-2 orders of teeth, 2-3 teeth/cm, regularly spaced, shape straight/concave to convex/straight to convex/convex, sinus rounded, apex simple. Primary venation pinnate, with 3 basal veins; compound agrophic veins present. Major secondary venation craspedodromous; secondary vein spacing irregular but tends to gradually increase proximally; secondary vein angle uniform; attachment to midvein excurrent; inter-secondaries absent. Tertiary venation opposite percurrent; tertiary vein angle obtuse to midvein; tertiary vein course straight to convex.

Remarks: This morphotype resembles fossil foliage from Svalbard referred to *Craspedodromophyllum malmgrenii* (HEER) GOLOVNEVA (GOLOVNEVA 2002; BUDANTSEV & GOLOVNEVA 2009). *Craspedodromophyllum* is a fossil-genus erected by CRANE (1981) to accommodate fossil foliage found in association with, but not connected to, the fossil fruit *Palaeocarpinus.* Although *Palaeocarpinus* has been reported from Svalbard, thus justifying the use of *Craspedodromophyllum* for the Spitsbergen leaf remains, no specimens of *Palaeocarpinus* have been found on Ellesmere or Axel Heiberg islands.

Nevertheless, the strong similarity between the Svalbard fossils referred to *Craspedodromophyllum malmgrenii* and the specimens from Ellesmere Island suggests these leaves may be the same taxon. Leaves similar to this morphotype have also been reported from the Ardtun flora on the Isle of Mull, but were included in *Corylites hebridicus* by BOULTER & KVAČEK (1989, p. 81, pl. 14, fig. 5). Our morphotype differs from leaves typically assigned to *Corylites hebridicus* in that the lamina of CAF-054 is wider basally, has fewer pairs of major secondary veins, and commonly displays large toothy projections along the margin.

Fossil foliage similar to, or referred to, *Craspedodromophyllum* has been reported from various mid- to high-latitude early Paleogene localities from North America, Svalbard, the Isle of Mull, and Russia (e.g., CRANE 1981 and references therein; BOULTER & KVAČEK 1989; SUN & STOCKEY 1992; GOLOVNEVA 2002; BUDANTSEV & GOLOVNEVA 2009; MOISEEVA et al. 2018).

Family FAGACEAE

Genus *Fagopsiphyllum* MANCHESTER

Fagopsiphyllum cf. *F. groenlandicum* (HEER 1868) MANCHESTER 1999

Morphotype CAF-065

Text-fig. 3.23, Pl. 9, Figs. 2–3

Morphotype exemplar: YPM PB 169838-7937

Localities: USPC 6, 105, 111, 200, 367; YPM 7937

Description: Leaf microphyllous to notophyllous, petiolate, attachment marginal, length-to-width ratio about 2:1, symmetrical; apex shape straight, apex angle acute; base shape convex, base angle acute. Leaf margin serrately crenate, with 1 order of teeth and 1-3 teeth/cm, regularly spaced, shape convex/concave to convex/convex, sinus rounded, apex simple. Primary venation pinnate, with 1 basal vein; agrophic veins absent. Major secondary venation craspedodromous; secondary vein spacing regular; secondary vein angle uniform; attachment to midvein decurrent to excurrent; inter-secondary veins absent. Tertiary venation opposite percurrent; tertiary vein angle obtuse to midvein; tertiary vein course straight.

Remarks: Leaves of *Fagopsiphyllum* MANCHESTER, *Fagopsis* HOLLICK, and *Fagus* L. are characterized by: elliptical shape; craspedodromous venation; straight, unbranched, evenly-spaced secondary veins; absent inter-secondary and agrophic veins; prominent, simple, non-glandular dentate or serrate teeth; and, very fine tertiary veins (MANCHESTER & CRANE 1983; BOULTER & KVAČEK 1989; MANCHESTER 1999; MANCHESTER & DILLHOFF 2004; GNILOVSKAYA & GOLOVNEVA 2016).

WOLFE (1977) transferred the fossil-species *Quercus groenlandica* HEER to *Fagopsis*, creating the new combination *Fagopsis groenlandica* (WOLFE) HEER. MANCHESTER (1999) noted that many fossil leaves assigned to *Fagopsis* were not found in association with crucial reproductive structures, which had been described in association with the type species *Fagopsis longifolia* (LESQUEREUX) HOLLICK. As a result, MANCHESTER (1999) established the fossil-genus of *Fagopsiphyllum* to accommodate fossil foliage that resembled *Fagopsis*, but was lacking associated reproductive material.

There is considerable morphological overlap between foliage assigned to *Fagopsis* and *Fagopsiphyllum*, and it has been suggested they may represent a single extinct taxon (GNILOVSKAYA & GOLOVNEVA 2016). BUDANTSEV & GOLOVNEVA (2009) felt there was no morphological difference between *Fagopsiphyllum* and *Quercus* L. and retained the original

binomial of *Quercus groenlandicum* HEER, rather than use *Fagopsiphyllum groenlandicum*.

Here we follow MANCHESTER (1999), referring these fossils to *Fagopsiphyllum,* as no reproductive material has been found in association with the Ellesmere Island specimens. Nevertheless, as this morphotype is described from limited material that was incomplete, the specific assignment remains tentative. Similar to other fossils referred to *Fagopsiphyllum* (i.e., GNILOVSKAYA & GOLOVNEVA 2016), the Ellesmere Island specimens display some polymorphism, primarily in the marginal dentition, which can vary from small, blunt teeth to large, triangular teeth.

Fagopsiphyllum, and the similar *Fagopsis,* have been described from the early Paleogene of North America, Greenland, Scotland, Svalbard, Russia, and Asia (HEER 1868; HOLLICK 1909; BROWN 1962; KOCH 1963; WOLFE 1977; MANCHESTER & CRANE 1983; BOULTER & KVAČEK 1989; TANAI 1995; BUDANTSEV 1997; MANCHESTER 1999; BUDANTSEV & GOLOVNEVA 2009; GRÍMSSON et al. 2016).

Family JUGLANDACEAE

Genus cf. *Carya* NUTT.

cf. '*Carya*' *antiquorum* NEWBERRY 1868

Morphotype CAF-014

Text-fig. 3.24, Pl. 9, Figs. 7–8

Morphotype exemplar: USPC 436-2749

Localities: USPC 111, 174, 175, 176, 178, 261, 436, 438

Description: Leaflets notophyllous to mesophyllous, possibly sessile, attachment marginal, elliptic, likely pinnately compound, length-to-width ratio about 3:1, asymmetrical; apex angle acute, apex shape straight to acuminate; base angle acute, base shape convex. Leaf margin serrate to serrately crenate to medially and basally untoothed, with 1 order of teeth, 3-4 teeth/cm, regularly spaced, shape concave/convex to concave/retroflexed to retroflexed/convex,

sinus angular, apex simple. Primary venation pinnate, with 1 basal vein; agrophic veins absent. Major secondary venation semicraspedodromous; secondary vein spacing irregular; secondary vein angle smoothing increasing proximally; attachment to midvein excurrent to partially decurrent; weak inter-secondary veins present. Tertiary venation opposite percurrent; tertiary vein angle obtuse to midvein; tertiary vein course straight to convex, with vein spacing irregular and vein angle smoothly decreasing.

Remarks: This morphotype resembles the fossil-species '*Carya*' *antiquorum* NEWBERRY (1868). Following MANCHESTER (1987), quotation marks are used for '*Carya' antiquorum* as the relationship to modern *Carya* NUTT. may be in error. The characteristics shared by this morphotype and '*Carya*' *antiquorum* include: small evenly spaced serrate teeth; semicraspedodromous secondary venation; well organized percurrent tertiaries; and, asymmetrical leaflets. Additionally, '*Carya*' *antiquorum* will commonly display regularly occurring marginal tertiary veins that extend perpendicularly from the secondary vein and then flex upwards when entering the teeth (MANCHESTER 1987), an architectural trait also observed in material from Ellesmere Island.

MANCHESTER (2001) notes that when only isolated leaflets are available, differentiating between *Aesculus* L. and *Carya* can be challenging. As such it is important to note that this morphotype does share similarities (e.g., asymmetry, small orderly serrate teeth, and semicraspedodromous secondary veins) to fossil material referred to *Aesculus longipedunculus* SCHLOEMER-JÄGER from Svalbard (SCHLOEMER-JÄGER 1958).

MANCHESTER (2001) notes a method for differentiating isolated leaflets of *Aesculus* and *Carya,* where *Aesculus* commonly has weakly impressed tertiary veins, while *Carya* and other Juglandaceous fossil foliage commonly have strongly impressed tertiary veins; however, in contrast to this observation, *Aesculus longipedunculus* is noted for having especially prominent tertiary veins (SCHLOEMER-JÄGER 1958). Furthermore, the fluvial and deltaic depositional environments common to Ellesmere and Axel Heiberg islands often taphonomically bias how

well higher orders of venation preserve, such that grades of vein preservation become less useful for distinguishing between morphologically similar fossil foliage from the Canadian palaeoarctic (C. K. WEST pers. obs.). These two factors further compound the difficulty in identifying isolated leaflets as either *Aesculus* or *Carya.*

Nevertheless, morphotype CAF-014 has a convex base rather than the decurrent base common to *A. longipedunculus,* precluding assignment of CAF-014 to this species. Additionally, this morphotype has secondary venation that is not as parallel, nor as well organized, nor as evenly spaced as observed in *A. longipedunculus* (SCHLOEMER-JÄGER 1958; BUDANTSEV & GOLOVNEVA 2009). This tendency to disorderly secondary venation is an architectural trait similar to that observed in other specimens also referred to *'Carya' antiquorum* (C. K. WEST pers. obs., see for example MANCHESTER 1987, p. 13, fig. 3-B). Given the complexity of identifying isolated leaflets as either *Aesculus* or *Carya*, the taxonomic assignment for this morphotype remains tentative.

Fossil forms attributed to *Carya* are common throughout the early Paleogene in North America (MANCHESTER 1987), although certain assignments (e.g., BROWN 1962; HICKEY 1977) have been found to represent forms of *Aesculus* rather than *Carya* (MANCHESTER 2014). Fossil material of Juglandaceous affinity has been identified from Greenland, Svalbard, and the Isle of Mull (HEER 1882; SCHLOEMER-JÄGER 1958; BOULTER & KVAČEK 1989; KVAČEK et al. 1994; BUDANTSEV & GOLOVNEVA 2009).

Family MYRICACEAE

Genus *Comptonia* L'HÉRITIERÉ ex W. AITON

Comptonia sp.

Morphotype CAF-069

Pl. 9, Figs. 9–10

Morphotype exemplar: USPC 164-4272

Localities: USPC 164

Description: Leaf microphyllous, petiolate, attachment marginal, elliptic, deeply lobed to pinnatisect, length-to-width ratio about 3-4:1, symmetrical; apex damaged but angle likely acute; base angle acute, base shape cuneate. Individual lobes are falcate to semioval; lobe apices rounded or acute; lobe sinuses rounded or angular; distal side of lobes straight to convex, proximal side of lobes convex. Margin untoothed. Primary venation pinnate, with 1 basal vein; agrophic veins absent. Major secondary venation craspedodromous; secondary vein spacing regular; secondary vein angle uniform.

Remarks: This morphotype is described from fragmentary and incomplete specimens; however, the distinctive foliage of *Comptonia* L'HÉRITIERÉ ex W. AITON is easily recognized by the elliptic, deeply lobed to pinnatisect lamina. Although no apices were preserved in the available specimens from Ellesmere and Axel Heiberg islands, it appears that the apex narrows acutely as in other fossil specimens of *Comptonia.* Limited material prevents a specific assignment for this morphotype.

Comptonia was widespread during the early Paleogene and has been reported from multiple mid- to high-latitude localities in North America (e.g., DAWSON 1890; BERRY 1906; HOLLICK 1936; WOLFE & WEHR 1987; MANCHESTER 1999; MCIVER & BASINGER 1999; SMITH et al. 2009; LIANG et al. 2010 and references therein).

Family INCERTAE SEDIS

Genus *Ushia* KOLAKOVSKIY

Ushia cf. *U. olafsenii* (HEER 1868) BOULTER et KVAČEK 1989

Morphotype CAF-027

Text-fig. 3.25, Pl. 9, Figs. 4–6

Morphotype exemplar: USPC 111-6157

Localities: USPC 6, 22, 23, 25, 105, 108, 111,166, 175, 196, 198, 200, 250, 251, 253, 255, 259,

261, 267, 371, 435, 436, 444, 657, 661, 708, 710, 711, 712, 716, 718, 752, 753, 757, 759, 1005, 1012, 1014

Description: Leaf microphyllous to mesophyllous, petiolate, attachment marginal, elliptic to ovate, length-to-width ratio about 1-2:1, symmetrical to weak basal asymmetry; apex shape straight to rounded, apex angle acute to obtuse; base shape concavo-convex to decurrent, base angle obtuse. Leaf margin serrate to serrately crenate, with 1-2 orders of teeth, 3-5 teeth/cm, regularly spaced, shape convex/concave to concave/concave to concave/retroflexed, sinus rounded, apex simple. Primary venation pinnate, with 1 basal vein; compound agrophic veins present. Major secondary venation craspedodromous; secondary vein spacing regular to decreasing distally; secondary vein angle uniform to increasing distally; attachment to midvein excurrent; inter-secondary veins absent. Tertiary venation opposite percurrent to mixed opposite alternate percurrent; tertiary vein angle obtuse to midvein; tertiary vein course convex.

Remarks: This morphotype shows strong resemblance to leaves previously referred to as *Ushia diplodon* (SAPORTA & MARION) PALAMAREV & MAI from Belgium, *Ushia olafsenii* (HEER) BOULTER et KVAČEK from the Isle of Mull and as *Rarytkinia quercifolia* (BUDANTSEV) GOLOVNEVA from Svalbard (BOULTER & KVAČEK 1989; PALAMAREV & MAI 1998; BUDANTSEV & GOLOVNEVA 2009).

The fossil-genus *Ushia* KOLAKOVSKIY was first described from the Paleocene of Kamyshin in the Volga River area of Western Eurasia as *Ushia kamyschinensis* KOLAKOVSKIY (KOLAKOVSKIY 1966; KRASSILOV et al. 1996); the fossil-genus has been used for leaves in many other early Paleogene localities from Central Eurasia, Europe, Alaska, Ireland, and Northern Russia (BOULTER & KVAČEK 1989; KRASSILOV et al. 1996; PALAMAREV & MAI 1998; COLLINSON & HOOKER 2003; AKHMETIEV 2010; MOISEEVA 2009, 2012).

Similarities between *Ushia* and the southern hemisphere genus *Nothofagus* BLUME have been noted, as well as similarities between the basal venation and some members of the Betulaceae, suggesting that *Ushia* may be a link to either *Nothofagus* or possibly the link

between the Betulaceae and Fagaceae (PALAMAREV & MAI 1998). *Ushia* is generally characterized by its elliptic shape, decurrent base, straight secondary veins, compound agrophic veins that have a tendency to loop before the margin, and ladder-like closely spaced tertiary veins (KOLAKOVSKIY 1966; BOULTER & KVAČEK 1989).

Multiple species of *Ushia* have been established to accommodate morphologically similar leaves from the mid to high latitudes in North America, Europe, and Russia (BOULTER & KVAČEK 1989; KRASSILOV et al. 1996; PALAMAREV & MAI 1998; BUDANTSEV & GOLOVNEVA 2009). Morphological characters typically used to differentiate between species of *Ushia* usually include the size of the lamina, the form of the marginal dentition, and the order of the secondary venation (BOULTER & KVAČEK 1989; KRASSILOV et al. 1996; PALAMAREV & MAI 1998; BUDANTSEV & GOLOVNEVA 2009).

BUDANTSEV & GOLOVNEVA (2009) suggested that the fossil-genus *Ushia*, originally described from a subtropical flora, would be an extremely unlikely member of the Arctic palaeoflora. Instead, BUDANTSEV & GOLOVNEVA (2009) preferred to use the alternative fossil-genus *Rarytkinia* VASSILEVSK et GOLOVNEVA for foliage resembling *Ushia* from the circumboreal and polar latitudes (BUDANTSEV & GOLOVNEVA 2009).

BUDANTSEV & GOLOVNEVA (2009) acknowledged that there are many similarities between *Ushia* and *Rarytkinia* (e.g., shape, margin, and tertiary venation) but suggested that certain differences between the two genera merit separation. *Rarytkinia* is noted as being larger and wider, with a broader base, blunter deltoid teeth, and gently curving secondary veins, whereas *Ushia* is described as being generally smaller, narrower, with sharper acute teeth, and straighter secondary veins (BUDANTSEV & GOLOVNEVA 2009).

However, fossil leaves from Ellesmere and Axel Heiberg islands share many of these architectural characters, display morphological overlap, and could be referred to either of these two form genera. Therefore, *Ushia* is retained as it was established prior to *Rarytkinia,* is the more common usage, and may be synonymous (e.g., BOULTER & KVAČEK 1989; KVAČEK et al.

1994; DENK et al. 1999; MCIVER & BASINGER 1999; UHL et al. 2007; KVAČEK 2010; GRÍMSSON et al. 2016). *Ushia* leaves from Ellesmere and Axel Heiberg islands are highly polymorphic and display a range of size, shape, basal and apical characteristics. Marginal dentition for these leaves is commonly either one order of shallow, subtle teeth, or less commonly two orders of larger deltoid teeth (e.g., pl. 9, fig. 5).

Although *Ushia* leaves from Ellesmere and Axel Heiberg Island resemble both *Ushia diplodon* and *Ushia olafsenii,* the latter species is preferred as it shares the most morphological features to the leaves from the Canadian Arctic; however, the specific assignment to *Ushia olafsenii* remains tentative due to the high degree of polymorphism.

Order Rosales

Family ROSACEAE

Genus cf. *Crataegus* TOURN. ex. L.

cf. *Crataegus* sp. 1

Morphotype CAF-101

Text-fig. 3.26, Pl. 9, Fig. 11, Pl. 10, Figs. 1–2

Morphotype exemplar: USPC 753-2075

Localities: USPC 753, 759

Description: Leaf microphyllous to notophyllous, petiolate, attachment marginal, ovate, length-to-width ratio about 2:1, symmetrical; apex shape straight, apex angle acute; base shape concave to truncate, base angle obtuse. Leaf margin toothed, serrate, with 2-3 orders of teeth, 3 teeth/cm, regularly spaced, shape convex/straight to straight/straight, sinus angular, apex simple. Primary venation pinnate, with 1 basal vein; agrophic veins absent. Major secondary venation is craspedodromous; secondary vein spacing regular; secondary vein angle uniform; attachment to midvein excurrent; inter-secondary veins absent. Tertiary venation opposite percurrent; tertiary vein angle obtuse to midvein; tertiary vein course convex to straight.

Remarks: The foliar morphology of these specimens is similar to some extant to forms of *Crataegus* TOURN. ex. L. (e.g., *Crataegus chrysocarpa* ASHE and *Crataegus submollis* SARG.), and to some forms of extant broad-leaved varieties of *Sorbus* L. (e.g., *Sorbus torminalis* (L.) CRANTZ, *Sorbus latifolia* (LAM.) PERS., and *Sorbus pseudosemiincisa* BOROS), as both genera demonstrate some similar foliar characteristics (e.g., shape, size, and serrate margins with compound teeth).

However, wider forms of *Sorbus* appear to be unknown from the early Paleogene in North America, and as such *Crataegus* is suggested for comparison. This assignment is based on foliar morphology and a limited number of fossil specimen; as a result, this assignment remains tentative.

Paleogene fossil leaves referred to *Crataegus* have been found in Alaska, British Columbia, and Washington State (HOLLICK 1936; WOLFE & WEHR 1987; DEVORE & PIGG 2007), and a fossil specimen referred to '*Crataegus*' *antiqua* HEER is known from Svalbard (BUDANTSEV & GOLOVNEVA 2009). *Crataegus* is unknown from the Isle of Mull.

cf. *Crataegus* sp. 2

Morphotype CAF-127

Text-fig. 3.27

Morphotype exemplar: USPC 367-3899

Localities: USPC 367

Description: Leaf mesophyllous, ovate, length-to-width ratio about 1.5:1, appears symmetrical but basal portion not preserved; apex shape appears straight but apex incomplete, apex angle acute. Leaf margin toothed, with 2 orders of teeth, 2-3 teeth/cm, regularly spaced, shape convex/convex to convex/straight, sinus angular, apex simple. Primary venation pinnate, with 1 basal vein likely. Major secondary venation craspedodromous; secondary vein spacing regular; secondary vein angle uniform; attachment to midvein excurrent; inter-secondary veins absent.

Tertiary venation opposite percurrent; tertiary vein angle obtuse to midvein; tertiary vein course convex.

Remarks: This large fossil leaf shares some morphological resemblance to leaves of extant forms of *Crataegus* (e.g., *Crataegus monogyna* JACQ. and *Crataegus pinnatifida* BUNGE), including the two orders of serrate teeth, and lobes that reach towards the midrib.

The lobes in morphotype CAF-127 appear to be restricted to the basal portion of the leaf. The lamina of CAF-127 narrows towards the midrib in the basal portion of the leaf, below this appears to be preserved a partially complete lobe with the same venation pattern. The base of the specimen is incomplete, thus the partially complete lobe could also be a leaflet, which would suggest that CAF-127 is pinnately compound rather than pinnately lobed.

The region of the lamina that narrows to the midrib does not narrow enough to suggest termination of the lamina and petiolar insertion for a subtending leaflet. The evidence suggests this leaf is similar to certain modern forms of *Crataegus,* although it is important to note this association is based on gross leaf morphology only, and as such the taxonomic assignment remains tentative.

Fossil leaves referred to *Crataegus* are reported from various localities in North America (e.g., HOLLICK 1936; WOLFE & TANAI 1980, WOLFE & WEHR 1987), but are rare from Svalbard (BUDANTSEV & GOLOVNEVA 2009), and unknown from the Isle of Mull.

Genus cf. *Sorbaria* (SER.) A. BRAUN

cf. *Sorbaria* aff. *S. wahrhaftigii* WOLFE et WEHR 1988

Morphotype CAF-079

Text-fig. 3.28

Morphotype exemplar: YPM PB 169817-8547

Localities: YPM 8547

Description: Leaflet microphyllous, elliptic, length-to-width ratio about 2.5:1, appears

symmetrical but basal portion not preserved; apex shape straight, apex angle acute. Leaf margin serrate, with 2-4 orders of teeth, 6 teeth/cm, regularly spaced, shape concave/concave to convex/concave, sinuses angular, apex simple. Primary venation pinnate, with 1 basal vein likely; agrophic veins absent. Major secondary venation craspedodromous; secondary vein spacing regular; secondary vein angle uniform; attachment to midvein excurrent; inter-secondary veins absent.

Remarks: This morphotype is described from a single specimen that has multiple orders of teeth, a feature commonly seen in members of extant Rosaceae (e.g., *Sorbus*, *Sorbaria* (SER.) A. BRAUN, and *Crataegus*). This morphotype resembles a fossil specimen from Spitsbergen described by KVAČEK et al. (1994) as being reminiscent of the Rosaceae.

KVAČEK et al. (1994) suggested a possible affinity to *Sorbus*, although they ultimately left the genus and species unassigned. This morphotype also closely resembles fossils assigned to *Sorbaria* from late Eocene/early Oligocene and Miocene deposits in Alaska (WOLFE & TANAI 1980; WOLFE & WEHR 1988). Damage to the specimen obscures whether the leaflets are paracompound and lacking intersecondary laminar segments (i.e., *Sorbaria*), or pinnatisect with intersecondary laminar segments, which would suggest a more primitive systematic position (e.g., *Stonebergia* WOLFE et WEHR; WOLFE & WEHR 1988).

Sorbus wahrhaftigii WOLFE et WEHR from the late Eocene/early Oligocene Rex Creek flora in Alaska can be recognized based on the presence of laminar hairs, tertiary vein pairs, laminar size, and the number of subsidiary teeth on the apical and basal flanks of major teeth (WOLFE & WEHR 1988). The Ellesmere Island morphotype is described from a single incomplete specimen that is poorly preserved (e.g., tertiary venation not visible). The Ellesmere Island leaflets commonly have 0-2 subsidiary teeth on the apical flank and 1-4 subsidiary teeth on the basal flank of major teeth, and measure approximately 2-3 cm long and 0.75-1.25 cm wide, although these measurements were made from incomplete leaflets and may represent minimum values.

Sorbaria wahrhaftigii commonly has 1-3 subsidiary teeth on the apical flank and 3-5 subsidiary teeth on the basal flank of major teeth, and typically measure 4.5-7.0 cm long and 3.5-6.0 cm wide (WOLFE & WEHR 1988). The similarities in morphological characteristics suggest that the Ellesmere Island material is likely *Sorbaria* and potentially related to the geologically younger *Sorbaria wahrhaftigii* from Alaska, but as the description is based on limited material the assignment remains tentative.

Taxa similar to CAF-079 (e.g. *Sorbaria* and *Stonebergia*) are known from British Columbia, Alaska, and Greenland in the early Paleogene (HEER 1869; WOLFE 1966; WOLFE & TANAI 1980; WOLFE & WEHR 1988).

Family ULMACEAE

Genus *Ulmus* L.

Ulmus ulmifolia (SCHLOEMER-JÄGER 1958) BUDANTSEV 1983

Morphotype CAF-012

Text-fig. 3.29, Pl. 10, Figs. 3–5, 8

Morphotype exemplar: USPC 200-4809

Localities: USPC 22, 105, 108, 111, 164, 200, 259, 435, 438, 439, 1014; YPM 7973, 8426

Description: Leaf microphyllous to mesophyllous, petiolate, attachment marginal, ovate to elliptic, length-to-width ratio about 2:1, symmetrical; apex shape convex to acuminate, apex angle acute; base shape rounded to cordate, base angle obtuse. Leaf margin serrate to serrately crenate, with 1-3 order of teeth, 1-6 teeth/cm, regularly spaced, shape is concave/concave to convex/straight to convex/convex, sinus angular, apex simple. Primary venation pinnate, with 1 basal vein; agrophic veins absent. Major secondary venation craspedodromous; secondary vein spacing regular to irregular; secondary vein angle uniform; attachment to midvein excurrent; inter-secondary veins absent. Tertiary venation alternate percurrent to opposite percurrent; tertiary vein angle obtuse to midvein; tertiary vein course straight to convex.

Remarks: This morphotype resembles fossil foliage referred to *Ulmus ulmifolia* (SCHLOEMER-JÄGER) BUDANTSEV (BUDANTSEV & GOLOVNEVA 2009). Shared characteristics include: an asymmetric base; an acute or acuminate apex; secondary veins that commonly bifurcate near the margin; broad, triangular, crenate teeth; and, a combination of simple and compound teeth (KVAČEK et al. 1994; BUDANTSEV & GOLOVNEVA 2009).

The polymorphism of this morphotype overlaps with contemporaneous fossil-species of *Ulmus* L. from mid-latitude fossil localities (e.g., the Okanagan Highlands of British Columbia Canada and Washington USA). Some specimens from Ellesmere Island (e.g., pl. 10, fig. 8) exhibit robust and deeply incised teeth, and also display serrate compound teeth, the primary teeth typically have a sharply acute apex, the basal flank of the tooth is typically convex while the apical flank is either concave or sigmoid. These morphological characteristics resemble *Ulmus chuchuanus* (BERRY) LAMOTTE, a species of elm from the Okanagan Highlands of British Columbia, Canada (BERRY 1926; LAMOTTE 1952; DENK & DILLHOFF 2005).

Other specimens from Ellesmere Island (e.g., pl. 10, figs. 3–5) have teeth that are distinctively deltoid in shape with blunt, rounded, or rarely acute apices, a suite of morphological characteristics that more resemble *Ulmus okanaganensis* DENK et DILLHOFF, another Eocene fossil-species from the Okanagan Highlands (DENK & DILLHOFF 2005).

The polymorphism observed in morphotype CAF-012 may also indicate that the late Paleocene - early Eocene forests on Ellesmere Island were populated by more than one species of elm tree; however, more likely the polymorphism reflects differences in leaf development, such as ‘sucker-shoot’ leaves, elongated vegetative shoot leaves, and short shoot leaves (sensu DENK & DILLHOFF 2005). This morphotype is referred to *Ulmus ulmifolia* as it strongly resembles other fossil foliage referred to this polar species of elm (KVAČEK et al. 1994; BUDANTSEV & GOLOVNEVA, 2009).

Fossil forms of *Ulmus* have been found in many early Paleogene localities at both high- and mid-latitudes in North America and Europe (BROWN 1962; WOLFE 1968, 1977; HICKEY

1977; BUDANTSEV 1983; KVAČEK et al. 1994; MCIVER & BASINGER 1999; DENK & DILLHOFF 2005; BUDANTSEV & GOLOVNEVA 2009; AKHMETIEV 2010).

Malvids

Order Sapindales

Family SAPINDACEAE

Genus *Aesculus* L.

Aesculus longipedunculus SCHLOEMER-JÄGER 1958

Morphotype CAF-038

Text-fig. 3.30, Pl. 10, Figs. 6–7, 9–10

Morphotype exemplar: USPC 111-4892

Localities: USPC 6, 105, 108, 111, 163, 169, 175, 195, 200, 261, 422, 433, 436, 439, 1005, 1012, 1014

Description: Leaflets notophyllous to mesophyllous, petiolate, attachment marginal, elliptic to obovate, likely palmately compound, length-to-width ratio about 2-4:1, symmetrical; apex shape convex or acuminate, apex angle acute; base shape decurrent, base angle acute. Leaf margin serrate, with 1 order of teeth, 3-5 teeth/cm, regularly spaced, shape is straight/convex to convex/convex to convex/straight, sinus angular to rarely rounded, apex simple. Primary venation pinnate, with 1 basal vein; agrophic veins absent. Major secondary venation craspedodromous to weakly semicraspedodromous; secondary vein spacing regular; secondary vein angle smoothly increasing proximally; attachment to midvein excurrent; inter-secondaries absent. Tertiary venation opposite percurrent; tertiary vein angle to midvein obtuse; tertiary vein course straight.

Remarks: This morphotype strongly resembles fossils from Svalbard referred to *Aesculus longipedunculus* based on the shape, the finely-serrate margin, secondary vein angle that increases proximally, a typically decurrent base, and when preserved, long petioles. *Aesculus*

longipedunculus is further identified by commonly having very robust strongly-impressed percurrent tertiary venation, a characteristic that separates it from *Aesculus hickeyi* MANCHESTER, a contemporaneous mid-latitude species of *Aesculus* which is noted for having weakly impressed and typically poorly preserved percurrent tertiary venation (KVAČEK et al. 1994; MANCHESTER 2001).

Although complete palmately compound specimens of *A. longipedunculus* have been reported from Svalbard (e.g., BUDANTSEV & GOLOVNEVA 2009, p. 358, pl. 75, fig. 3), no such specimens have been recovered from Ellesmere Island. Nevertheless, the available evidence supports assignment of this morphotype to *Aesculus longipedunculus.*

Fossils referred to *Aesculus* have been found in contemporaneous deposits on Svalbard (SCHLOEMER-JÄGER 1958; BUDANTSEV 1983; KVAČEK et al. 1994; GOLOVNEVA 2000; BUDANTSEV & GOLOVNEVA 2009), and from fossil localities from mid-latitude North America (e.g., BROWN 1962; HICKEY 1977; MANCHESTER 2001).

Order *Incertae sedis*

Family *INCERTAE SEDIS*

Genus *Averrhoites* HICKEY

Averrhoites cf. *A. affinis* (NEWBERRY 1868) HICKEY 1977

Morphotype CAF-067

Text-fig. 3.31, Pl. 10, Figs. 11, Pl. 11, Fig. 1

Morphotype exemplar: USPC 178-4161

Localities: USPC 177, 178; YPM 7920

Description: Leaflets microphyllous to notophyllous, petiolate, attachment marginal, likely pinnately compound, elliptic to ovate, length-to-width ratio about 2:1, basally asymmetrical, medially asymmetrical to symmetrical; apex shape acuminate, apex angle acute; base shape concave, base angle acute. Leaflet margin untoothed. Primary venation pinnate, with 1 basal

vein; agrophic veins absent. Major secondary venation brochidodromous to weakly brochidodromous; secondary vein spacing irregular to regular; secondary vein angle uniform; attachment to midvein excurrent; weak inter-secondary veins present.

Remarks: The specimens assigned to this morphotype are brochidodromous, untoothed, appear chartaceous or waxy, and are likely pinnately compound. The characteristics are similar to fossil leaves previously referred to *Averrhoites* HICKEY, a genus established by HICKEY (1977) for foliage previously referred to *Sapindus affinis* (NEWBERRY) BROWN.

Fossil leaves figured by BROWN (1962, p. 226, pl. 47, fig. 3) belonging to *Averrhoites affinis* (NEWBERRY) HICKEY (= *Sapindus affinis*) demonstrate a pinnately compound laminar organization, an architectural character not observed in any specimen from Ellesmere Island. However, the Ellesmere Island specimens were typically found clustered close together, but rarely intact, suggesting that the leaflets were disarticulated during transportation.

HICKEY (1977) suggested a possible affinity to the Oxalidaceae for *Averrhoites*; however, the higher taxonomic affinity of this genus is currently uncertain. The fragmentary and poorly preserved nature of the specimens recovered from Ellesmere Island obscure the necessary architectural characters (i.e., higher order venation) required to firmly refer this fossil morphotype to the species *Averrhoites affinis*; as such the taxonomic assignment of this morphotype remains tentative.

Averrhoites has been previously reported from early Paleogene mid-latitude localities (e.g., NEWBERRY 1868; BROWN 1962; HICKEY 1977; MCIVER & BASINGER 1993), Alaska (HOLLICK 1936, p. 262, pl. 76, fig. 5), and Russia (MOISEEVA et al. 2018), but has not been reported from Svalbard or the Ardtun flora from the Isle of Mull.

Genus aff. *Celastrinites* SAPORTA

aff. *Celastrinites* sp.

Morphotype CAF-131

Text-fig. 3.32, Pl. 11, Fig. 4

Morphotype exemplar: USPC 111-4917

Localities: USPC 111, 261

Description: Leaf microphyllous, length-to-width ratio about 2:1 but lamina incomplete, appears medially asymmetrical; apex shape straight, apex angle acute. Leaf margin poorly preserved. Primary venation pinnate, 1 basal vein apparent; agrophic veins absent. Major secondary veins appear brochidodromous or craspedodromous; secondary vein spacing irregular; secondary vein angle uniform; attachment to midvein excurrent; inter-secondary veins absent. Tertiary venation mixed opposite-alternate percurrent; tertiary vein angle obtuse to midvein.

Remarks: This morphotype was described from two incomplete specimens. The preserved architectural characters are similar to those of fossil foliage from Svalbard referred to *Celastrinites septentrionalis* (KRYSHTOFOVICH) GOLOVNEVA (BUDANTSEV & GOLOVNEVA 2009, p. 248, pl. 20, fig. 2–4), a fossil-species with uncertain taxonomic affinity at the family level. The limited number of specimens from which this morphotype was described precludes a firm taxonomic assignment at this time. As such we suggest only affinity to *Celastrinites* SAPORTA. Similar fossil leaves have also been reported from Northern Russia (MOISEEVA 2009, 2012).

Genus cf. *Cornophyllum* NEWBERRY

cf. *Cornophyllum* sp.

Morphotype CAF-032

Text-fig. 3.33

Morphotype exemplar: USPC 438-2791

Localities: USPC 438

Description: Leaf notophyllous, appears ovate but both apical and basal portions of lamina damaged, length-to-width ratio about 1:1, appears symmetrical; apex angle appears acute; base

angle obtuse, base shape appears rounded. Margin is untoothed. Primary venation is pinnate, with 1 basal vein; agrophic veins absent. Major secondary venation eucamptodromous; secondary vein spacing decreasing proximally; secondary vein angle uniform; attachment to midvein excurrent; inter-secondary veins absent.

Remarks: Poor preservation prevents a robust description of this fossil, as many of the architectural characters are not preserved; however, the entire, slightly erose margin and the eucamptodromous secondary veins that curve uniformly towards the apex are characteristic of leaves commonly referred to *Cornus* L. However, some eucamptodromous fossil leaves previously referred to *Cornus* are now excluded as they either have prominent irregular teeth or lack the necessary preserved calcified double-armed acicular trichomes that are diagnostic of *Cornus* (MANCHESTER 2014).

The preserved architectural characters suggest that an assignment to *Cornus* may be appropriate, and the specimen does bear some similarity to *Cornus hyperborea* HEER from Greenland (HEER 1869); however, as this morphotype is based on a single, damaged, untoothed, eucamptodromous specimen without preserved calcified double-armed acicular trichomes, an association to Cornaceae is uncertain. The fossil-genus *Cornophyllum* NEWBERRY is used instead for leaves of this morphotype, although the species remains uncertain.

Fossils referred to *Cornus* are relatively rare in early Paleogene fossil localities, but have been reported from North America, Svalbard, Greenland, and Russia (e.g., HEER 1869; BROWN 1962, HICKEY 1977; BUDANTSEV & GOLOVNEVA 2009; MANCHESTER et al. 2009; MOISEEVA et al. 2018), although the association of some of these fossils to Cornaceae may be spurious (MANCHESTER et al. 2009).

Genus *Macclintockia* HEER

Macclintockia sp.

Morphotype CAF-149

Pl. 11, Fig. 5

Morphotype exemplar: USPC 168-4270

Localities: USPC 168

Description: Leaf, incomplete, appears microphyllous, length-to-width ratio about 2:1, appears symmetrical; base shape cuneate, base angle acute. Leaf margin untoothed. Primary venation actinodromous.

Remarks: This morphotype was described from a single specimen recovered from Strand Fiord on Axel Heiberg Island that strongly resembles similar fragments previously referred to the fossil-genus *Macclintockia* HEER (e.g., BUDANTSEV & GOLOVNEVA 2009). The taxonomic affinities of this leaf are unknown, but they have been reported from Greenland, Svalbard, and the Ardtun Flora form the Isle of Mull (HEER 1868; BOULTER & KVAČEK 1989; BUDANTSEV & GOLOVNEVA 2009; GRÍMSSON et al. 2016).

Genus *Quereuxia* KRYSHTOFOVICH ex BAIKOVSKAJA

Quereuxia angulata (NEWBERRY 1861) KRYSHTOFOVICH 1953

Morphotype CAF-105

Pl. 11, Figs. 2–3, 6–8

Morphotype exemplar: USPC 191-3967

Localities: USPC 23, 169, 191, 193, 253, 370, 358, 359, 360, 361, 362, 363, 364, 367, 441, 442, 443, 444

Description: Leaf nanophyllous to microphyllous, simple and compound, may form rosettes, petiolate, attachment marginal, obovate to elliptical to ovate, length-to-width ratio about 1:1, symmetrical to basally asymmetrical; apex shape rounded, apex angle obtuse; base shape rounded to truncate to weakly cordate. Leaf margin serrate, with 1 order of teeth, 7-10 teeth/cm, regularly spaced, shape concave/convex to concave/straight to concave/flexuous, sinus rounded, apex simple or glandular, possibly mucronate. Primary venation pinnate to appearing

actinodromous, with 1-5 basal veins; agrophic veins absent. Major secondary venation is craspedodromous; secondary vein spacing irregular; secondary vein angle uniform; attachment to midvein excurrent; inter-secondary veins rarely present. Rhizomes present, 2-3 mm wide, 3-8 cm long; nodes occur along rhizomes at intervals of about 2.5 cm; rhizome leaves present, bladeless, highly dichotomized; roots present, elongate, up to 1.5 cm long, curving or branched from nodal intersections; possible bud scales observed, up to 1 cm long, apparent parallel veins converging towards apex.

Remarks: This morphotype strongly resembles material previously referred to the fossil-species *Quereuxia angulata* (NEWBERRY) KRYSHTOFOVICH and is easily recognized by its distinctive small serrate leave as well as the associated rhizomes, rhizome leaves, and root complexes often preserved with the fossil leaves. Previous studies have determined that these aquatic dicots likely grew from a submerged rhizome system and occupied the margins of freshwater ponds, swamps and fluvial systems (STOCKEY & ROTHWELL 1997).

The fossil-genus *Quereuxia* KRYSHTOFOVICH ex BAIKOVSKAJA has a complicated nomenclatural history (see HICKEY 2001), and fossil material referred to this genus has been previously referred to either the extant genus *Trapa* L. or the fossil-genus *Trapago* MCIVER et BASINGER—now a junior synonym for *Quereuxia* (MCIVER & BASINGER 1993; HICKEY 2001; MANCHESTER 2014). The association to the family Trapaceae is considered unlikely, and as such the familial affinity of this hydrophyte remains unresolved.

This distinctive floating plant is well known from localities across North America and Asia, ranging from the upper Cretaceous through to the Paleocene (LESQUEREUX 1878; WARD 1887; BERRY 1935; BROWN 1962; HICKEY 1977; MCIVER & BASINGER 1993; STOCKEY & ROTHWELL 1997; MANCHESTER 2014; MOISEEVA et al. 2018), but has not been reported from either Svalbard or the Ardtun flora from the Isle of Mull.

gen indet. sp. indet.

Morphotype CAF-016

Text-fig. 3.34, Pl. 11, Figs. 9–11

Morphotype exemplar: USPC 436-2769.1

Localities: USPC 363, 436, 442

Description: Leaf microphyllous to mesophyllous, petiolate, attachment marginal, obovate, length-to-width ratio about 1.5-2:1, symmetrical to basally symmetrical; apex shape convex to rounded, apex angle obtuse; base shape rounded to convex to cuneate, base angle obtuse to acute. Leaf margin serrate to serrately crenate, with 1 order of teeth, 4-7 teeth/cm, regularly spaced, shape convex/straight to convex/concave to convex/convex, sinus angular, apex simple. Primary venation pinnate, with 1 basal vein; compound agrophic veins present. Major secondary venation craspedodromous; secondary vein spacing irregular; secondary vein angle uniform; attachment to midvein excurrent to rarely distally decurrent; inter-secondary veins absent. Tertiary venation opposite percurrent; tertiary vein angle obtuse to perpendicular to midvein; tertiary vein course convex.

Remarks: This morphotype is characterized by obovate leaves, prominent primary venation that begins robustly in the basal portion of the leaf and diminishes towards the apex, strong compound agrophic veins, a serrate margin with multiple small teeth that gives the margin a slightly 'chewed' or ‘saw-tooth’ appearance, and a combination of noticeably off-set and opposite to sub-opposite major secondary veins.

This morphotype appears to resemble the lateral leaflets of *Platanites marginata* (LESQUEREUX) JOHNSON (= *Cissus marginata* (LESQUEREUX) BROWN) figured by BROWN (1962, p. 237, pl. 54, fig. 4), as well as other solitary leaves that BROWN (1962) felt were representative of discarded lateral leaflets and should, therefore, be combined into this genus (e.g., KNOWLTON 1930, p. 170, pl. 23, fig. 3); however, as the lateral leaflets are considered highly polymorphic it is difficult to refer the Ellesmere Island specimens to *P. marginata* without additional fossil evidence (e.g., a convincing terminal leaflet belonging to *P.*

marginata).

While it is possible that these leaves may represent the discarded lateral leaflets of some hitherto undiscovered form of polar *Platanites*, the current taxonomic assignment remains uncertain.

gen. indet. sp. indet.

Morphotype CAF-024

Text-fig. 3.35

Morphotype exemplar: USPC 436-2752.1

Localities: USPC 436

Description: Leaf mesophyllous, petiolate, attachment marginal, obovate, length-to-width ratio about 2:1, symmetrical; base shape rounded, base angle obtuse. Leaf margin serrate, with 1 order of teeth, 5 teeth/cm, regularly spacing, shape is straight/flexuous to convex/concave, sinus angular, apex simple. Primary venation suprabasal actinodromous, with 7 basal veins; simple agrophic veins present. Major secondary venation is craspedodromous to semicraspedodromous; secondary vein spacing irregular; secondary vein angle uniform; inter-secondary veins present, inter-secondary vein course perpendicular to midvein. Tertiary venation mixed opposite alternate percurrent; tertiary vein angle obtuse to midvein; tertiary vein course convex to chevron.

Remarks: This morphotype is represented by a single large leaf with several unique architectural characters, including: suprabasal actinodromous venation with seven basal veins; the petiolar insertion point to the primary veins is very robust; and, a distinctively serrated margin. It appears this leaf may have been folded or damaged during deposition; however, enough distinct architectural characters remain that designate the leaf as a unique morphotype. The taxonomic affinity of this morphotype remains unresolved.

gen. indet. sp. indet.

Morphotype CAF-025

Text-fig. 3.36

Morphotype exemplar: USPC 439-2801

Localities: USPC 439

Description: Leaf mesophyllous, appears ovate but apical portion of leaf not preserved, length-to-width ratio about 1:1, symmetrical; base shape appears cordate but basal portion of leaf damage, base angle reflexed. Leaf margin serrate with 1 order of teeth, 2 teeth/cm, regularly spaced, shape convex/concave, sinus rounded to angular, apex simple. Primary venation likely pinnate but midvein not preserved; simple agrophic veins present. Major secondary venation craspedodromous; secondary vein spacing regular; secondary vein angle uniform; inter-secondary veins absent. Tertiary venation opposite percurrent; tertiary vein angle to midvein obtuse; tertiary vein course straight.

Remarks: Although incomplete, the large, sharp, serrate teeth of this fossil are unique amongst the fossil flora of Ellesmere Island. The lack of preserved characters prevents this specimen from being assigned a taxonomic affinity.

gen. indet. sp. indet.

Morphotype CAF-033

Text-fig. 3.37

Morphotype exemplar: USPC 436-2735.1

Localities: USPC 436

Description: Leaf mesophyllous, sessile, attachment marginal, elliptic, length-to-width ratio about 2:1, weak basal asymmetry; apex shape convex, apex angle acute; base shape rounded, base angle acute. Leaf margin serrate, with 1 order of teeth, 8 teeth/cm, regularly spaced, shape is straight/convex, sinus rounded, apex simple. Primary venation pinnate, with 1 basal vein; compound agrophic veins present. Major secondary venation craspedodromous; secondary vein

spacing irregular; secondary vein angle uniform; attachment to midvein excurrent; inter-secondary veins absent. Tertiary venation opposite percurrent; tertiary vein angle obtuse to midvein; tertiary vein course straight.

Remarks: This specimen is characterized by its strong elliptic shape, irregularly spaced secondary venation, a serrate margin with very fine teeth that give an appearance that the margin is untoothed, disorderly secondary venation, and weak inter-secondary veins. Additionally, the position of the petiolar insertion suggests this leaf may have been sessile—although this could be a preservational artifact.

Although this morphotype shares some similarities with morphotype CAF-016, the fine-toothed margin and the irregular, disorderly secondary venation distinguishes it from morphotype CAF-016.

gen. indet. sp. indet.

Morphotype CAF-063

Text-fig. 3.38

Morphotype exemplar: YPM PB 169831-8432

Localities: YPM 8432

Description: Leaf microphyllous, attachment marginal, appears ovate but lamina incomplete; base shape cordate, base angle reflexed. Leaf margin serrately crenate, with 1 order of teeth, 2 teeth/cm, regularly spaced, shape convex/convex, sinus angular, apex simple. Primary venation pinnate, with 5 basal veins; agrophic veins absent. Major secondary venation craspedodromous; secondary vein spacing irregular; secondary vein angle uniform; attachment to midvein excurrent; weak inter-secondary veins present. Tertiary venation mixed opposite-alternate percurrent; tertiary vein angle obtuse to midvein.

Remarks: This morphotype is based on a single fragmentary specimen that is characterized by pinnate venation with crowded basal secondary veins, large crenate teeth that are medially

enervated by a major or minor secondary vein, and tertiary veins from the basal-most major secondary veins that loop before the margin. This suite of foliar characteristics is not observed in any other fossil leaf from Ellesmere or Axel Heiberg Islands, and as such is established as a distinct morphotype.

gen. indet. sp. indet.

Morphotype CAF-070

Text-fig. 3.39

Morphotype exemplar: YPM PB 169855-8437

Localities: YPM 8437

Description: Leaf notophyllous, attachment marginal, ovate, length-to-width ratio about 1.5:1, symmetrical; apex angle appears acute but apex is damaged; base shape rounded, base angle obtuse. Leaf margin serrate, with 1 order of teeth, 4 teeth/cm, regularly spaced, shape convex/straight, sinus angular, apex simple. Primary venation pinnate, with 3 basal veins; compound agrophic veins present. Major secondary venation craspedodromous; secondary vein spacing gradually increasing proximally and abruptly decreasing at base; secondary vein angle uniform; attachment to midvein excurrent; inter-secondary veins absent. Tertiary venation opposite percurrent, tertiary vein angle obtuse to midvein, tertiary vein course convex.

Remarks: This morphotype is described from a single incomplete specimen; however, unique venation differentiates this morphotype from other Ellesmere Island leaf fossils. Most noticeably, the distance between the major secondary veins along the midvein increases gradually towards the base. This pattern is abruptly interrupted near the base, as the distance between the ultimate and the penultimate secondary veins shortens dramatically. Narrowing of the lamina in the apical portion of the leaf suggests this morphotype had an acute apex.

The agrophic veins of this morphotype are also uniquely organized. The basal comb of agrophic veins extends towards the margin but appears to curve apically to form brochidodromous loops; whereas, the distal agrophic comb is strongly craspedodromous, with

veins that curve towards the apex before reaching the margin to enervate teeth.

Although the suite of morphological characters of this fossil leaf differentiate it from other Ellesmere Island fossil flora, the morphotype was described from a single incomplete specimen, and taxonomic affinity remains uncertain.

gen. indet. sp. indet.

Morphotype CAF-073

Text-fig. 3.40, Pl. 12, Fig. 1

Morphotype exemplar: YPM PB 169867-8418

Localities: USPC 175; YPM 8418

Description: Leaf mesophyllous, petiolate, attachment marginal, elliptic, length-to-width ratio about 2:1, symmetrical; apex shape straight, apex angle acute; base shape convex, base angle obtuse. Leaf margin dentate, with 1 order of teeth, 2-3 teeth/cm, regularly spaced, shape concave/retroflexed to flexuous/retroflexed, sinus angular, apex simple. Primary venation pinnate, with 1 basal vein; agrophic veins absent. Major secondary venation semicraspedodromous; secondary vein spacing regular; secondary vein angle uniform; attachment to midvein excurrent; inter-secondary veins absent. Tertiary venation opposite percurrent; tertiary vein angle obtuse to midvein; tertiary vein course with a convex to sinuous.

Remarks: This morphotype can be recognized by its elliptic shape, small dentate teeth, secondary veins that bifurcate near the margin to form loops and enervate teeth along the margin, and the widely spaced, opposite, percurrent tertiary venation. These characteristics are reminiscent of leaves aligned with Juglandaceae; however, as this morphotype was described from a single specimen, the taxonomic affinities of this morphotype remain unresolved.

gen. indet. sp. indet.

Morphotype CAF-076

Text-fig. 3.41

Morphotype exemplar: YPM PB 169805-8441

Localities: YPM 8441

Description: Leaf microphyllous, petiolate, attachment marginal, ovate, palmately lobed, length-to-width ratio about 1:1, appears symmetrical although apical portion of leaf poorly preserved; apex angle acute; base shape truncate, base angle obtuse. Leaf margin appears untoothed but is poorly preserved. Primary venation basal actinodromous, with 5 basal veins; agrophic veins present. Major secondary venation is brochidodromous; secondary vein spacing gradually increases proximally; secondary vein angle uniform; attachment to midvein excurrent; inter-secondary veins absent. Tertiary venation opposite percurrent; tertiary vein angle to midvein obtuse; tertiary vein course convex.

Remarks: This morphotype was described from a single specimen, and is distinctive due to the actinodromous venation, the deeply incised lobes, and brochidodromous secondary veins. Morphotype CAF-076 is differentiated from leaves referred to *Archeampelos* by the brochidodromous secondary venation, a character not observed in *Archeampelos.* Furthermore, the lobes of morphotype CAF-076 are deeply incised, whereas the lobes of Ellesmere Island *Archeampelos* are shallower.

The actinodromous venation and the presence of lobes are characters considered basal to the genus *Acer* (WOLFE & TANAI 1987). Although this combination of architectural characters suggests a possible affinity to *Acer*, the poor preservation of the margin and a lack of higher order venation precludes a taxonomic assignment of this morphotype.

gen. indet. sp. indet.

Morphotype CAF-100

Text-fig. 3.42

Morphotype exemplar: YPM PB 169928-7973

Localities: YPM 7973

Description: Leaf notophyllous, elliptic, petiolate, attachment marginal; base angle obtuse, base shape rounded. Leaf margin appears untoothed, but only basal portion preserved. Primary venation suprabasal acrodromous, with 3 basal veins; agrophic veins absent. Major secondary venation appears brochidodromous; secondary vein spacing irregular; secondary vein angle uniform; attachment to midvein decurrent; basal fimbrial vein present; inter-secondary veins present. Tertiary venation alternate percurrent; tertiary vein angle obtuse to midvein.
Remarks: This morphotype is described from a single fragmentary specimen. The middle and apical portion of the lamina are missing; however, the exaggerated suprabasal acrodromous venation, a fimbrial vein, and an untoothed margin suggest an affinity to the Lauraceae. There is some resemblance between morphotype CAF-100 and leaves assigned to *Oreodaphne obtusifolia* BERRY (1916, p. 301, pl. 83, fig. 3), a common element of the Wilcox Flora (DILCHER 1963) which was subsequently transferred to *Ocotea* AUBL. by LAMOTTE (1952), and later confirmed by cuticular analyses (DILCHER 1963). Despite this resemblance, the morphotype is based on a single specimen and is both fragmentary and poorly preserved, which precludes a firm taxonomic assignment at this time.

These fossil leaves are similar to other leaves with suprabasal acrodromous venation also found on Ellesmere Island, which have been referred to *Trochodendroides crenulata*; however, the distance between the first and second set of basal veins is greatly reduced in leaves of *T. crenulata*, and a fimbrial vein is lacking.

No fossil leaves assigned to Lauraceae have been recovered from Svalbard, nor from the sub-Arctic Ardtun flora from the Isle of Mull, although leaves referred to *Cinnamomum* SCHÄFFER were described from Alaska (HOLLICK 1936), possible Lauraceous leaves from Greenland (GRÍMSSON et al. 2016), and *Ocotea* has also been reported from Russia (AHKMETIEV 2007). Lauraceous fossil leaves have also been identified from mid-latitude Paleogene localities in North America (e.g., BROWN 1962).

gen. indet. sp. indet.

Morphotype CAF-103

Text-fig. 3.43

Morphotype exemplar: YPM PB 169925-7962

Localities: YPM 7962

Description: Leaf microphyllous, petiolate, attachment marginal, elliptic, length-to-width ratio about 3:1, symmetrical; base shape convex, base angle acute. Margin untoothed. Primary venation pinnate, with 1 basal vein; agrophic veins absent. Major secondary venation poorly preserved but appears craspedodromous. Higher order venation not preserved.

Remarks: This morphotype is described from a single sample with multiple preserved leaves. The untoothed margin, robust primary vein, a short petiole, and a long, thin, elliptic lamina differentiates this morphotype from other fossil flora reported from Ellesmere Island.

Major secondary and higher venation are not preserved on the majority of the specimens; however, what appears to be secondary veins are preserved on one of the basal portions of a specimen. These veins appear to consist of several pairs of craspedodromous veins. The taxonomic affinity of this morphotype remains uncertain due to the limited material available for study.

gen. indet. sp. indet.

Morphotype CAF-104

Text-fig. 3.44

Morphotype exemplar: USPC 175-4113

Localities: USPC 175, 442

Description: Leaf nanophyllous, petiolate, attachment marginal, appears elliptical but incomplete, length-to-width ratio about 2:1, appears symmetrical but apical portion of leaf not preserved; base shape concave, base angle acute. Margin is untoothed. Primary venation

pinnate, with 1 basal vein; agrophic veins absent. Major secondary venation appears brochidodromous but is poorly preserved.

Remarks: This morphotype is described from a nearly complete single specimen. The lamina is notable for its small size, elliptic shape, apparent brochidodromous secondary veins, and untoothed margin. The secondary veins are poorly preserved and appear to diverge from the primary vein and reach toward the margin before looping to join the superjacent secondary veins. Without additional specimens, it is impossible to suggest a taxonomic affinity for this morphotype, but is it significant, as untoothed margins are rare in the Canadian Arctic flora.

gen. indet. sp. indet.

Morphotype CAF-130

Text-fig. 3.45, Pl. 12, Fig. 9

Morphotype exemplar: USPC 200-4771

Localities: USPC 200

Description: Leaf microphyllous, petiolate, attachment marginal, elliptic, length-to-width ratio about 2:1, symmetrical; apex angle appears acute but apex incomplete; base angle acute, base shape convex. Leaf margin serrate, with 1 order of teeth, 2 teeth/cm, regularly spaced, shape convex/convex to convex/concave, sinus rounded, apex simple. Primary venation suprabasal actinodromous, with 3 basal veins; agrophic veins absent. Major secondary venation craspedodromous; secondary vein spacing irregular; secondary vein angle inconsistent with two pairs of acute basal secondary veins; attachment to midvein weakly deflected; inter-secondary veins absent. Tertiary venation opposite percurrent; tertiary vein angle obtuse to midvein; tertiary vein course convex.

Remarks: This morphotype is described from a single specimen that includes both part and counterpart of a compressed leaf fossil. This morphotype is superficially similar to morphotype CAF-016 in vein organization; however, the large teeth suggest that this fossil leaf should be considered distinct from other fossil morphotypes described from Ellesmere Island. Despite the

distinctiveness of this fossil, without additional specimens the taxonomic affinities of this morphotype remain undetermined.

gen. indet. sp. indet.

Morphotype CAF-132

Text-fig. 3.46

Morphotype exemplar: USPC 111-4933

Localities: USPC 111

Description: Leaf microphyllous to notophyllous, attachment marginal, ovate, length-to-width ratio about 1.5:1, appears symmetrical; apex angle appears acute but incomplete; base shape cordate, base angle obtuse. Leaf margin untoothed. Primary venation pinnate, with 1 basal vein; agrophic veins absent. Major secondary venation brochidodromous; secondary vein spacing regular; secondary vein angle smoothly increasing proximally to rarely inconsistent; attachment to midvein excurrent; inter-secondary veins absent. Tertiary venation opposite percurrent; tertiary vein angle obtuse to midvein; tertiary vein course convex.

Remarks: This morphotype is described from two specimens and is characterized by an ovate shape, untoothed margin, and brochidodromous secondary venation. This suite of architectural characteristics differentiates morphotype CAF-132 from the other fossil foliage of Ellesmere Island. The specimens are incomplete and cannot be assigned a taxonomic affinity at this time.

gen. indet. sp. indet.

Morphotype CAF-134

Pl. 12, Figs. 2–3

Morphotype exemplar: USPC 436-2733

Localities: USPC 436

Description: Leaf notophyllous, attachment peltate excentric, likely orbicular or ovate but leaf damaged and incomplete; length-to-width ratio about 1:1; base shape lobate to rounded, base

angle circular to reflexed. Leaf margin untoothed. Primary venation basal actinodromous, with 10-12 basal veins; agrophic veins absent. Major secondary venation brochidodromous; secondary vein spacing irregular; secondary vein angle uniform; attachment to midvein excurrent; inter-secondary veins absent. Tertiary venation alternate percurrent; tertiary vein angle obtuse to perpendicular to midvein.

Remarks: The peltate excentric position of lamina attachment, the basal acintodromous venation, and the large number of basal veins differentiate this morphotype from the other Ellesmere Island morphotypes. The fossils do bear some superficial resemblance to extant *Nymphaea* L. and to fossils previously referred to this genus; however, the petiolar attachment position of CAF-134 is peltate excentric, rather than centrally peltate as occurs in *Nymphaea.*

Furthermore, the abundance of broad-leaf deciduous fossil leaves found in association with these specimens, rather than fossils indicative of an aquatic habitat, suggest the depositional environment was unsuitable for aquatic plants. Finally, the presence of undulations and ripples in the sediment suggest that the depositional system may have been the result of a flow or flooding event (e.g., flood plain or crevasse splay) inundating the forest floor. The available evidence suggests that a relationship to *Nymphaea* would be unlikely.

This morphotype also bears some resemblance to foliage of extant members of Menispermaceae. The extant species *Stephania cephalantha* HYATA and *Cissampelos owariensis* BEAUV ex DC are both woody climbing plants that produce untoothed, peltate excentric leaves, with a large number of primary veins. The association with Menispermaceae, though tenuous, is certainly plausible given that Menispermaceae began to rapidly diversify in North America during the Eocene (MANCHESTER 1999), whereas fossil foliage attributed to Nymphaceae remained rare (MANCHESTER 1999, 2014).

Much of the fossil foliage from North America originally attributed to Menispermaceae, such as *Cocculus* DC. and *Menispermites* LESQUEREUX (HICKEY 1977), are now considered to belong to *Nordenskioeldia*—an extinct plant with trochodendraceous affinity (CRANE et al.

1991; MANCHESTER et al. 1991), although many early Paleogene fossil leaves from North America retain an assignment to the Menispermaceae (JACQUES 2009 and references therein). Ultimately, as the specimens used to describe this morphotype were incomplete and few in number, the taxonomic assignment for this morphotype remains unresolved.

gen. indet. sp. indet.

Morphotype CAF-151

Text-fig. 3.47

Morphotype exemplar: USPC 171-4260

Localities: USPC 171

Description: Leaf microphyllous, petiolate, elliptic, length-to-width ratio about 2:1, symmetrical; apex shape rounded, apex angle acute; base shape rounded, base angle obtuse. Leaf margin untoothed. Primary venation pinnate, with 1 basal vein; agrophic veins absent. Major secondary venation brochidodromous; secondary vein spacing irregular; secondary vein angle uniform, attachment to midvein decurrent; inter-secondary veins absent. Tertiary venation appears opposite percurrent but poorly preserved.

Remarks: This morphotype was described from a single specimen. Untoothed leaves are uncommon in the Ellesmere and Axel Heiberg islands flora.

gen. indet. sp. indet.

Morphotype CAF-086

Pl. 12, Figs. 4–5, 7

Morphotype exemplar: USPC 6-498

Localities: USPC 6, 105, 111, 196, 198, 430, 435, 442, 753, 712

Description: Probable infructescence pedunculate, found unattached, singly, or rarely as branched pairs; peduncle 6-10 mm long, 2-3 mm wide, bearing a shortened branching system composed of 4 or 5 pedicels, possibly helically arranged, each pedicel bearing 2-3 probable

follicles; pedicels tightly grouped proximally and may appear as a single structure but divisions observable, individual pedicels about 0.5 mm wide, about 3-6 mm long; probable follicles 6-10 mm long, elliptic or ovate, may appear forked or notched apically.

Remarks: This morphotype was described from numerous specimens and is interpreted as a condensed infructescence, which consists of a shortened ovulate branching system bearing clusters of follicles. The infructescence appears to be unisexual, as no evidence was preserved to suggest that it may have been bisexual. MCIVER & BASINGER (1999, p. 533, fig. 17) figured a specimen now assigned to this morphotype and suggested it may be cercidiphyllaceous.

Similar fossils reported from Svalbard were referred to the fossil-genus *Palaeanthus* NEWBERRY by BUDANTSEV & GOLOVNEVA (2009), who interpreted these fossils as a fagaceous or fagaceous-like cupule. The specimens from Ellesmere Island, however, do not preserve evidence of a receptacle, bracts, or dehisced valves as would be expected for a fagaceous cupule, which suggests that this interpretation is unlikely.

The pedicels of the follicles may appear fused proximally in poorly preserved specimens, which may then be misinterpreted as a single unified structure or a floral receptacle; however, in well preserved specimens the axes appear as distinct but tightly grouped independent structures. The taxonomic affinities of these specimens remain unresolved pending further taxonomic review.

gen. indet. sp. indet.

Morphotype CAF-123

Pl. 12, Fig. 6

Morphotype exemplar: YPM PB 169888-8418

Localities: YPM 8418

Description: Possible catkin, about 25 mm long but appears incomplete, about 1.5-3 mm wide, with central axis about 1 mm wide, bearing 14 pairs of leafy or floral projections. Leafy or

floral projections with acute apex, 0.5-2 mm long, about 0.5 mm wide, decreasing in size distally, appear opposite, open at 45° to central axis and flex downwards, each pair resembles a pair of flexed wings.

Remarks: This morphotype was described from a single specimen and may represent a poorly preserved or incomplete catkin. It is differentiated from similar morphotypes (e.g., CAF- 137) by the leafy or floral structures found along the central axis that open at 45° angles and then flex downward. This creates a distinctive visual appearance similar to pairs of bird wings in flight.

gen. indet. sp. indet.

Morphotype CAF-124

Pl. 12, Fig. 8

Morphotype exemplar: USPC 111-4922

Localities: USPC 111

Description: Possible catkin, about 40 mm in length but possibly incomplete, 7.5 mm wide; appears pluriflor, spicate; floral structures appear sessile, helical, overlapping. Bract-like structures triangular; bract apex acuminate.

Remarks: This morphotype was described from a single specimen and appears to be part of a catkin displaying numerous apetalous sessile flowers or bracts; however, the fossil is incomplete. The architecture of this fossil allows it to be easily differentiated from other reproductive material preserved from Ellesmere Island, but as the morphotype was described from a single specimen the taxonomic affinities of this fossil remain unresolved.

gen. indet. sp. indet.

Morphotype CAF-137

Pl. 13, Fig. 1

Morphotype exemplar: USPC 438-2786

Localities: USPC 438

Description: Possible catkin or leafy branchlet, incomplete, leafy or floral projections extend orthogonally from a central axis; leafy or floral projections 2-3 mm long, about 1-1.5 mm wide, narrow apically, appear to curve or hook near apex; central axis 13 mm long, about 1.5 mm wide, appears horizontally sectioned, ringed, or as stacked discs, each section about 1 mm thick.

Remarks: This morphotype was described from a single incomplete specimen and as such the taxonomic affinities of this fossil remain unresolved.

gen. indet. sp. indet.

Morphotype CAF-146

Pl. 13, Fig. 4

Morphotype exemplar: USPC 111-4924

Localities: USPC 111

Description: Possible inflorescence, incomplete; axis 20 mm long, 6 mm wide, bearing small, bract-like structures, helically arranged.

Remarks: This morphotype was described from a single specimen that appears to represent a possible inflorescence.

gen. indet. sp. indet.

Morphotype CAF-147

Pl. 13, Fig. 2

Morphotype exemplar: USPC 261-6317

Localities: USPC 261

Description: Possible inflorescence, incomplete; axis 20 mm long, 1-2 mm wide, bearing helically arranged structures, elliptic, apices appear acute.

Remarks: This morphotype was described from a single specimen that appears to represent a possible inflorescence.

gen. indet. sp. indet.

Morphotype CAF-093

Pl. 13, Figs. 3 & 6

Morphotype exemplar: USPC 261-6115

Localities: USPC 261

Description: Large fruit, apparent drupe, incomplete, about 55 mm long, 47 mm at widest point, appears elliptic. Pyrene about 43 mm long, 28 mm wide, elliptic, surface appears smooth but dimpled. Mesocarp striated, about 10 mm thick. Possible exocarp about 1.5 mm in thickness, but poorly preserved.

Remarks: This morphotype appears to be a large fleshy drupe, the pyrene and apparent mesocarp are well preserved but do not appear to display any significant architectural or cellular detail. It is possible the exocarp may have also been preserved; the sedimentary fabric of the matrix surrounding the fossil exhibits a change in lithology. This layer is approximately 2-4 mm in thickness, but as it is not continuous and occasionally indistinct, it is possible this may simply be a preservational artifact.

This morphotype is a unique element of the Ellesmere Island fossil flora and was described from a single specimen. The taxonomic affinities of this morphotype remain unresolved, but the fossil bears some superficial resemblance to a modern drupe.

gen. indet. sp. indet.

Morphotype CAF-138

Pl. 13, Fig. 5

Morphotype exemplar: USPC 22-1217

Localities: USPC 22

Description: Seeds dispersed, small, shape ovate or elliptic or oblong, 1-2 mm long, 0.5-0.8 mm wide; apex appears acute or blunted, but may result from poor preservation or damage; base

appears obtuse.

Remarks: Though poorly preserved, these seeds appear to thicken towards the base, which may represent the seed body. These seeds are easily differentiated from other seeds reported from Ellesmere Island based on their shape.

gen. indet. sp. indet.

Morphotype CAF-142

Pl. 13, Figs. 10 & 13

Morphotype exemplar: USPC 436-2776

Localities: USPC 436

Description: Seeds dispersed and possibly clustered, commonly occurring in groups of 6 or 8, organized as overlapping rows of 3 or 4 seeds, appear aligned along a central axis, possibly connected by short stalks; seeds 1-2.5 mm long, 1-2 mm wide, ovoid or renniform, may appear striated or dimpled.

Remarks: These seeds are distinctive and may appear freely dispersed or as apparently organized overlapping clusters of 6 or 8 seeds. Larger clusters were also found that suggest the seeds may have originally been part of a larger reproductive structure.

gen. indet. sp. indet.

Morphotype CAF-143

Pl. 13, Fig. 12

Morphotype exemplar: USPC 169-3981

Localities: USPC 169

Description: Possible seeds, 8-10 mm long, about 5-7 mm wide, shape ovoid or elliptic, apex obtuse, base obtuse; appear smooth, possibly keeled or bearing a single robust striation.

Remarks: These fossils appear to be preserved seeds and are distinctive from other seeds based on their size.

gen. indet. sp. indet.

Morphotype CAF-145

Pl. 13, Fig. 11

Morphotype exemplar: USPC 111-4920

Localities: USPC 111

Description: Probable reproductive structures, appear to be clustered woody fruits or fertile scales, 3 mm long, 2 mm wide; apex acute, rounded; base obtuse, round; shape ovoid, striated; appear ornamented with spines or projections.

Remarks: This fossil is described from a single specimen that appears to be preserved reproductive structures. The body of the fossil appears connected or tightly grouped and appears to contain woody fruits or fertile scales which appear to be ornamented with possible spines or projections. As this morphotype was described from a single specimen, it remains challenging to determine its taxonomic affinity and nature.

gen. indet. sp. indet.

Morphotype CAF-140

Pl. 13, Figs. 7–8

Morphotype exemplar: USPC 436-2747

Localities: USPC 436

Description: Possible short shoots or spur shoots, 19-25 mm long, 2-3.5 mm wide, shape elliptic; main vegetative body appears nodose; attached to apparently incomplete base, base 8-10 mm long, about 4 mm wide, appears swollen.

Remarks: These fossils possibly represent the vegetative short shoot system or spur of an unknown plant from Ellesmere Island. *Ginkgo* and morphotypes assigned to Cercidiphyllaceae (e.g., *Archeampelos* or *Trochodendroides*) and some conifers such as *Pseudolarix* GORDON are plants that produce such short shoot systems. Nevertheless, as these fossils were not found in

association with fossil foliage, it is not possible to taxonomically assign this morphotype.

gen. indet. sp. indet.

Morphotype CAF-141

Pl. 13, Fig. 9

Morphotype exemplar: USPC 436-2773

Localities: USPC 436

Description: Possible bract, obovate, 4-7 mm long, 5-7 mm wide distally, 2-4 mm wide proximally, appears longitudinally striated or veined; distal edge toothed, teeth regular, straight, sinus rounded, sharply acute, possibly spinose.

Remarks: These fossils appear to be bracts and were found in association with a leaf fragment that appears to be *Archeampelos*. Despite some superficial resemblance to CAF-144, this morphotype remains taxonomically unassigned as limited diagnostic information is available to suggest an affinity.

3.6 Discussion

The study of the early Paleogene floras from Ellesmere and Axel Heiberg islands contributes significantly to our understanding of polar floristics, floristic evolution, and environments during a time of global warmth. In the absence of permanent ice, or even significant winter frost at low elevations, polar forests thrived throughout the north polar regions.

The late Paleocene – early Eocene floras of the High Arctic were initially described as the ‘Arctic Miocene Floras’ by HEER (1868, 1869, 1870, 1876, 1878a), and subsequently described as the Arctotertiary Flora by ENGLER (1882; see MAI 1995). ENGLER (1882, page 137) defined the Arctotertiary Flora as a flora that is “distinguished by numerous conifers and genera of trees and shrubs that now dominate in North America or extratropical Europe”.

Simultaneously, ENGLER (1882) also defined a counterpart to the Arctotertiary Flora, the Palaeotropical Flora, which was comprised of floral elements found in the Old Word Tropics. In each case, these floral concepts were defined in terms of ecological and floristic elements (MAI 1991).

The similarities of the Arctotertiary Flora to the modern mixed deciduous flora common throughout North America and Europe led to an evolutionary framework, which developed into the "geoflora" concept. The widespread Arcto-Tertiary Geoflora was considered a high-latitude broad-leaved deciduous forest of exceptional ecological tolerance that subsequently migrated southward during the cooling near the end of the Paleogene, yet retained a typically consistent composition over geologic time (CHANEY 1947, 1959; MAI 1991). The southward migration of the Arcto-Tertiary Geoflora led to the development of the Arctic origin hypothesis, where many modern plant genera first appeared at high latitudes (CHANEY 1959; SPICER et al. 1987). WOLFE (1975), however, strongly criticized this idea and argued that the Geoflora concept was invalid, and would later propose the term Polar Broad-leaved Deciduous Forest for these ubiquitous early Cenozoic forests (WOLFE 1985; SPICER et al. 1987).

KVAČEK (1994) tested the Geoflora concept by evaluating the composition and distribution of floral elements common to the Arctic Paleogene. He concluded that the Paleogene Arctic vegetation could no longer be explained by a uniform Arcto-Tetiary Geoflora, as the constituent elements of the Paleogene Arctic vegetation reflected diverse histories that formed a mosaic of vegetational types.

GRÍMSSON et al. (2015) would also explore the Geoflora concept, and further concluded not only that the Geoflora concept must be rejected, but also that the idea of a polar origination for modern plant families should be rejected, as they found that many first occurrences predate middle Eocene fossil plant records at high latitudes.

Fossil evidence demonstrates that compositionally similar polar broad-leaved deciduous forests occupied much of the Paleogene high latitudes in North America (i.e., the Canadian

Arctic and Alaska), as well as Svalbard, Greenland, Scotland, Ireland and Russia (HOLLICK 1936; BOULTER & KVAČEK 1989; MCIVER & BASINGER 1999; AKHMETIEV 2007; BUDANTSEV & GOLOVNEVA 2009; HERMAN et al. 2009; MOISEEVA et al. 2009; KVAČEK 2010; GRÍMSSON et al. 2016).

Floristically similar floras are also known from the mid-latitudes of North America (e.g., Alberta, British Columbia, Montana, North Dakota, Saskatchewan, and Wyoming) (e.g., BROWN 1962; HICKEY 1977; MCIVER & BASINGER 1993; MANCHESTER 1999; COLLINSON & HOOKER 2003; PIGG & DEVORE 2010; GREENWOOD et al. 2005, 2016; LOWE et al. 2018). The similarities in composition of these floras suggest that the many ubiquitous floral members dominating the Canadian Arctic may have merged with elements of mid-latitude regions in North America during the early Paleogene.

Although previous studies have investigated the palaeobiogeography, dispersal routes, and floristic provinces of early Paleogene vegetation in North America and Europe at both high and mid-latitudes (e.g., MANCHESTER 1999; COLLINSON & HOOKER 2003; KVACEK 2010), we briefly discuss below some contemporaneous fossil floral assemblages, and provide summaries of the most common elements of those floras. It should be noted that these lists are not exhaustive and are meant to provide examples of the similarities between the late Paleocene – early Eocene Canadian Arctic Flora and the contemporaneous fossil floras from high-latitudes, and mid-latitudes of North America, Europe, and eastern Russia.

The complex of compositionally similar fossil floras of Greenland, the Isle of Mull, and Svalbard are first briefly discussed and compositional similarities with respect to the Canadian Arctic Flora are summarized. Following this, the fossil floras of Alaska and eastern Russian are discussed and summarized. Finally, some contemporaneous floras from the mid-latitudes of North America are also briefly discussed and summarized.

The late Paleocene fossil floras from Greenland are well documented, the most well-known are those from the Nuussuaq Basin in western Greenland (HEER 1868, 1869, 1882;

KOCH 1963, 1964; GRÍMSSON 2016), and the Thyra Ø flora from northern Greenland (BOYD 1990). These floras appear to have had a lower diversity than the fossil floras documented from Axel Heiberg and Ellesmere islands. The Greenland floras are typified by *Metasequoia*, *Macclintockia*, *Corylites*, and *Trochodendroides* (KOCH 1963; COLLINSON & HOOKER 2003; KVAČEK 2010). Additional dicotyledonous elements, similar to the Canadian Arctic Flora, include: *Fagopsiphyllum*, *Platanus*, and *Ushia* (COLLINSON & HOOKER 2003; KVAČEK 2010; GRÍMSSON 2016).

The late Paleocene British Tertiary Igneous Province flora from the Isle of Mull represents a flora similar to the fossil floras of Greenland (BOULTER & KVAČEK 1989; COLLINSON & HOOKER 2003; KVAČEK 2010). Similar to Greenland, the Isle of Mull flora contains *Macclintockia*, *Corylites*, and *Trochodendroides* (BOULTER & KVAČEK 1989); however, unlike Greenland, *Metasequoia* was a rare floral element of the Mull flora (KVAČEK 2010). Compositional elements from the Isle of Mull similar to the Canadian Arctic Flora include the ferns *Osmunda* and *Coniopteris* (≈ *Dennstaedtia*); gymnosperms such as *Ginkgo*, *Glyptostrobus*, and *Elatocladus*; and additional dicotyledonous fossil plants such as *Platanites*, *Fagopsiphyllum* (= *Fagopsis*), *Vitiphyllum*, and *Ushia* (BOULTER & KVAČEK 1989; KVAČEK 2010).

The late Paleocene – early Eocene floras on Svalbard, mainly those from Spitsbergen, were first described by HEER (1868, 1870, 1876). Subsequent studies have revisited the megaflora collections and much of the flora has been revaluated and re-described by SCHWEITZER (1974), KVAČEK & MANUM (1993), KVAČEK et al. (1994), and BUDANTSEV & GOLOVNEVA (2009). Similar to both Greenland and the Isle of Mull, the Spitsbergen fossil floras contain occurrences of *Metasequoia*, *Macclintockia*, *Corylites*, and *Trochodendroides* (BUDANTSEV & GOLOVNEVA 2009). Common floral elements similar to the Canadian Arctic Flora include: the ferns *Osmunda* and *Coniopteris*; the gymnosperms *Ginkgo*, *Glyptostrobus*, *Thuja*, and *Elatocladus*; and dicotyledonous elements such as *Nyssdium*, *Nordenskiodia*, *Ulmus*,

Fagopsiphyllum (as *Quercus*), *Aesculus,* and *Archeampelos* (as *Acer*) (KVAČEK et al. 1994; BUDANTSEV & GOLOVNEVA 2009).

The late Paleocene – early Eocene forests growing on the North Slope of Alaska typically contained *Metasequoia, Macclintockia*, *Corylites,* and *Trochodendroides* (WOLFE 1966, 1977; SPICER et al. 1987). Similar to the Canadian Arctic, the floras of Alaska contained occurrences of the fern *Osmunda* and the horsetail *Equisetum*, the conifer *Glyptostrobus,* and broad-leaved deciduous taxa such as *Archeampelos*, *Carya, Aesculus* and fossils referred to Arecaceae, Betulaceae, Fagaceae, and Sapindaceae (WOLFE 1966; SPICER et al. 1987; SUNDERLIN et al. 2011). The Sagwon Flora, another early Paleogene fossil flora of Alaska, was dominated by similar genera, but with notable additions such as: *Onoclea* L., *Quereuxia, Nyssidium arcticum*, *Ushia* (= *Rarytkinia*), *Celastrinites*, and *Corylites* (HERMAN et al. 2009; MOISEEVA et al. 2009).

During the late Paleocene–early Eocene, eastern Russia was connected to Alaska by the Bering Land Bridge, and similarities are apparent between the floras of the North Slope of Alaska and those of east Siberia and far eastern Russia (MANCHESTER 1999; COLLINSON & HOOKER 2003; AKHMETIEV 2007; HERMAN et al. 2009; MOISEEVA et al. 2009). These Russian floras were also dominated by *Metasequoia, Corylites,* and *Trochodendroides* (COLLINSON & HOOKER 2003). Similar floral elements to the Canadian Arctic flora include the fern *Coniopteris* (≈ *Dennstaedtia*), gymnosperms such as *Ginkgo and Glyptostrobus*, and dicotyledonous elements such as *Alnus*, *Platanus*, *Magnolia, Quereuxia*, and fossils attributed to Ulmaceae (GOLOVNEVA 1996; AKHMETIEV 2007, 2010; AKHMETIEV & BENIAMOVSKI 2006; MOISEEVA 2009).

The late Paleocene – early Eocene floras of North America are primarily found in the Williston, Green River, Powder River, Bighorn and Alberta Basins of the Great Plains and Rocky Mountains (PIGG & DEVORE 2010), as well as southern British Columbia (GREENWOOD et al. 2005, 2016). These floras typically contain similar compositional elements to the Polar

Broad-leaf Deciduous Forests, such as: *Osmunda*, *Equisetum*, *Ginkgo*, *Metasequoia*, *Glyptostrobus*, *Corylites*, *Cercidiphyllum*/*Joffrea*/*Trochodendroides*, *Archeampelos*, *Ulmus*, *Nyssidium*, *Platanus*, and *Aesculus* (BROWN 1962; CHANDRASEKHARAM 1974; CHRISTOPHEL 1976; HICKEY 1977; MCIVER & BASINGER 1993; MANCHESTER 1999; PIGG & DEVORE 2010; GREENWOOD et al. 2005, 2016), demonstrating a number of similar compositional elements to the fossil forests of the Canadian Arctic.

The most common floral elements of the palaeoarctic forests from Northernmost Canada appear to be *Equisetum*, *Metasequoia*, *Glyptostrobus*, *Nyssidium*, *Trochodendroides*, *Ushia*, *Ulmus*, *Archeampelos*, *Aesculus*, *Quereuxia*, and *Vitiphyllum*. These taxa have been recovered from most localities across both Ellesmere and Axel Heiberg islands, and nearly all these taxa can be found at late Paleocene – early Eocene fossil localities elsewhere in the High Arctic. Furthermore, many of these taxa can also be found at contemporaneous fossil sites from the middle latitudes of North America, with some notable exceptions (e.g., *Ushia*). This would seem to suggest that the Polar Broad-leaf Deciduous Forest was not only a circumpolar feature of the early Paleogene world (cf. KVAČEK 2010), but may have also mixed compositionally with the mid-latitudes as previously suggested (e.g., MANCHESTER 1999; COLLINSON & HOOKER 2003).

Morphotypes from the Canadian Arctic Flora referred to 'dicot' genera such as *Crataegus*, *Macginitiea*, and *Sorbaria* suggest that the mid-latitude floras of North America may have exchanged floral elements with the paleoarctic forests of Alaska, and Axel Heiberg and Ellesmere islands, as these are genera not recorded from other Paleogene high-latitude fossil sites.

The presence of fossil leaves from Ellesmere Island referred to *Tetracentron* supports previous suggestions of a dispersal route for this genus across the Bering Land Bridge from Asia (e.g., GRÍMSSON & DENK 2007; GRÍMSSON et al. 2008; MANCHESTER et al. 2009; DENK et al. 2011); and provides evidence for the idea that *Tetracentron* would have migrated northward

through Ellesmere Island to eventually colonize Iceland in the Miocene, as suggested by GRÍMSSON et al. (2008).

Those morphotypes described here from the Ellesmere and Axel Heiberg islands late Paleocene to early Eocene floras that remain unassigned to existing taxa may eventually be identified to taxa from contemporaneous high or mid-latitude fossils sites. If this proves to be the case, these additional records would demonstrate a greater degree of uniformity for these forests. Nevertheless, these unidentified elements suggest a certain degree of floral endemism exists within the paleoarctic forests of Ellesmere and Axel Heiberg islands.

Finally, it is important to note that stratigraphic age control of the early Paleogene sediments on Ellesmere and Axel Heiberg islands remains challenging. The fossiliferous formations that make up the Eureka Sound Group typically overlap considerably in age, are often lithologically similar, time transgressive or have been tectonically deformed. Supporting palynological evidence seems to suggest a late Paleocene to early Eocene age range for diverse localities (see KALKREUTH et al. 1993)

Age control is improved at certain localities (e.g., Stenkul Fiord, Strathcona Fiord, and Split Lake) by either vertebrate palaeontology or radiometric dating (DAWSON 1990, 2001; HARRINGTON et al. 2012; EBERLE & MCKENNA 2002; REINHARDT et al. 2013, 2017). Some localities may contain plant taxa that may be somewhat restricted in age, and therefore more indicative of either a Paleocene or Eocene age (e.g., *Macclintockia* or *Macginitiea*). Thus, it is possible to suggest that a specific locality more likely reflects the late Paleocene (e.g., *Macclintockia* is found at Strand Fiord) or early Eocene (e.g., *Macginitiea* is found at Stenkul Fiord, where age of some beds is controlled by relative and absolute dating); however, in most cases the fossil megaflora typically occur either stratigraphically well above or below the relative and absolute age tie points. Additionally, fossil localities from the same formation may be geographically separated, making bio-correlation challenging. As the ranges of the age-indicative floral elements are not well constrained, the potential for error suggests it would be

unwise to apply a more precise age to any locality at this time.

Future work for the Arctic localities will involve improved age control that will likely result in many of the localities used for this study to be eventually regarded as either late Paleocene or early Eocene, and as such new interpretations of the flora will be possible.

3.7 Conclusions

The late Paleocene–early Eocene megafloral fossil assemblage from Axel Heiberg and Ellesmere islands (Arctic Canada) presented here represents the high latitude polar forests of the early Cenozoic in Canada. The descriptions of plant morphotypes and morphotaxa presented here represent the first comprehensive taxonomic analysis of the late Paleocene–early Eocene Arctic Canada floras since the late 1800's (e.g., HEER 1878a).

Eighty-three plant megaflora morphotypes were described, of these 65 are angiosperm (62 'dicots' and 3 monocotyledonous) morphotypes. The remaining 18 megafloral morphotypes are comprised of 13 gymnosperms and 5 pteridophyte morphotypes. The morphotypes represent 17 orders and 22 families; however, 31 taxa remain of unknown affinity, many of which comprise the rarer elements of the flora. Dominant families within the Ellesmere and Axel Heiberg islands flora include: Cupressaceae, Cercidiphyllaceae, Betulaceae, Platanaceae, Fagaceae, Sapindaceae, and the Vitaceae. Rare elements with assigned affinities include the Magnoliaceae, Nelumbonaceae, Myricaceae, Juglandaceae, and the Rosaceae.

The similarity of this fossil flora to other contemporaneous fossil localities from both high- and mid-latitude localities from the late Paleocene and early Eocene suggests that these polar forests represent a circumpolar feature of the late Paleocene and early Eocene that may have exchanged elements with mid-latitude forests. These fossils serve as proxies for early Paleogene polar climate and contribute to our understanding of polar floristics, floristic evolution, and environments during a time of global warmth.

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Table 3.1:

Morph Number	Family	Taxa	Stenkul Fiord Area	Split Lake	Strand Fiord	Strathcona Fiord	Fosheim South	Fosheim North	Judge Daly Promontory	Lake Hazen
CAF-082	Equisetaceae	*Equisetum* sp.	1	1	0	1	1	1	1	1
CAF-119	Osmundaceae	*Osmunda macrophylla*	0	0	1	0	0	1	1	0
CAF-150	Salviniaceae	*Azolla* sp.	0	0	0	1	0	0	0	0
CAF-084	Salviniaceae	*Salvinia* cf. *S. preauriculata*	1	0	0	0	0	0	0	0
CAF-081	Dicksoniaceae	*Coniopteris blomstrandii*	0	0	1	0	0	1	1	1
CAF-110	Ginkgoaceae	*Ginkgo adiantoides*	1	0	1	1	1	0	0	1
CAF-115	aff. Pinaceae	CAF-115	1	0	0	0	0	0	0	0
CAF-109	Cupressaceae	cf. *Cunninghamia* sp.	0	0	0	1	0	0	0	0
CAF-107	Cupressaceae	*Metasequoia occidentalis*	1	1	1	1	1	1	1	1
CAF-108	Cupressaceae	*Glyptostrobus nordenskioldii*	1	1	0	1	1	1	1	1
CAF-111	Cupressaceae	*Elatocladus cordillera*	1	0	0	0	1	0	0	0
CAF-135	Cupressaceae	*Thuja polaris*	0	0	0	0	0	1	0	0
CAF-121	Cupressaceae	*Cupressinocladus* sp. 1	0	0	0	0	1	0	0	0
CAF-136	Cupressaceae	*Cupressinocladus* sp. 2	0	0	0	0	1	1	1	0
CAF-085	Incertae sedis	CAF-085	0	0	0	0	1	0	0	0
CAF-148	Incertae sedis	CAF-148	0	0	0	0	0	0	0	1
CAF-152	Incertae sedis	CAF-152	0	0	1	0	0	0	0	0
CAF-139	Incertae sedis	CAF-139	0	0	0	0	1	0	0	0
CAF-102	aff. Magnoliaceae	*Magnolia* sp.	0	0	1	0	1	0	0	1
CAF-118	Zingiberaceae	*Zingiberopsis* cf. *Z. isonervosa*	1	0	1	0	0	1	0	0
CAF-096	Incertae sedis	CAF-096	0	0	0	0	0	0	0	0
CAF-133	Incertae sedis	CAF-133	1	0	0	0	0	0	0	0
CAF-072	Nelumbonaceae	cf. *Nelumbo* sp.	1	0	0	1	0	0	0	0
CAF-080	Platanaceae	*Macginitiea* aff. *M. nobilis*	1	0	1	1	0	0	0	0
CAF-126	Platanaceae	*Macginicarpa* cf. *M. manchesteri*	1	0	0	0	0	0	0	0
CAF-128	Platanaceae	*Platanus* sp.	0	0	0	1	1	0	0	0
CAF-112	Trochodendraceae	*Nordenskioeldia borealis*	1	0	0	0	1	0	0	1
CAF-040	Trochodendraceae	*Tetracentron* cf. *T. hopkinsii*	0	0	0	1	0	1	0	0
CAF-034	Cercidiphyllaceae	*Archeampelos* cf. *A. acerifolia*	1	0	1	0	0	1	0	1
CAF-088	Cercidiphyllaceae	*Nyssidium arcticum*	1	0	1	1	1	0	0	1
CAF-035	Cercidiphyllaceae	*Trochodendroides arctica*	1	1	1	0	1	1	0	1
CAF-036	Cercidiphyllaceae	*Trochodendroides curvidens*	1	0	1	0	1	1	0	0

Morph Number	Family	Taxa	Stenkul Fiord Area	Split Lake	Strand Fiord	Strathcona Fiord	Fosheim South	Fosheim North	Judge Daly Promontory	Lake Hazen
CAF-021	Cercidiphyllaceae	*Trochodendroides crenulata*	1	1	1	0	1	1	0	0
CAF-098	Cercidiphyllaceae	*Trochodendroides richardsonii*	1	0	1	0	1	1	0	1
CAF-144	Incertae sedis	CAF-144	0	0	0	0	1	1	0	0
CAF-004	aff. Vitaceae	*Vitiphyllum* cf. *V. sewardii*	1	1	1	1	0	1	1	1
CAF-061	Betulaceae	*Alnus* cf. *A. parvifolia*	0	0	0	0	1	0	1	1
CAF-091	Betulaceae	*Alnus* sp.	0	0	0	1	1	0	0	1
CAF-031	Betulaceae	cf. *Paracarpinus* sp.	1	0	0	0	0	1	0	0
CAF-129	Betulaceae	*Corylites hebridicus*	0	0	0	1	1	1	0	1
CAF-054	Betulaceae	*Craspedodromophyllum* cf. *C. malmgrenii*	0	1	0	0	1	1	0	0
CAF-065	Fagaceae	*Fagopsiphyllum* cf. *F. groenlandicum*	0	0	0	1	1	1	0	0
CAF-014	Juglandaceae	cf. '*Carya*' *antiquorum*	1	0	1	0	1	0	0	1
CAF-069	Myricaceae	*Comptonia* sp.	1	0	0	0	0	0	0	0
CAF-027	Incertae sedis	*Ushia* cf. *U. olafsenii*	1	1	1	1	1	1	1	1
CAF-101	Rosaceae	cf. *Crataegus* sp. 1	0	0	0	0	0	0	1	0
CAF-127	Rosaceae	cf. *Crataegus* sp. 2	0	0	0	1	0	0	0	0
CAF-079	Rosaceae	cf. *Sorbaria* aff. *S. wahrhaftigii*	1	0	0	0	0	0	0	0
CAF-012	Ulmaceae	*Ulmus ulmifolia*	1	0	1	0	1	1	0	0
CAF-038	Sapindaceae	*Aesculus longipedunculus*	1	0	1	1	1	1	0	1
CAF-067	Incertae sedis	*Averrhoites* cf. *A. affinis*	0	0	1	0	0	0	0	0
CAF-131	Incertae sedis	aff. *Celastrinites* sp.	0	0	0	0	1	0	0	1
CAF-032	Incertae sedis	cf. *Cornophyllum* sp.	1	0	0	0	0	0	0	0
CAF-149	Incertae sedis	*Macclintockia* sp.	0	0	1	0	0	0	0	0
CAF-105	Incertae sedis	*Quereuxia angulata*	0	1	1	1	1	1	0	0
CAF-016	Incertae sedis	CAF-016	1	1	0	1	0	0	0	0
CAF-024	Incertae sedis	CAF-024	1	0	0	0	0	0	0	0
CAF-025	Incertae sedis	CAF-025	1	0	0	0	0	0	0	0
CAF-033	Incertae sedis	CAF-033	1	0	0	0	0	0	0	0
CAF-063	Incertae sedis	CAF-063	0	0	0	0	1	0	0	0
CAF-070	Incertae sedis	CAF-070	0	0	0	1	0	0	0	0
CAF-073	Incertae sedis	CAF-073	1	0	1	0	0	0	0	0
CAF-100	Incertae sedis	CAF-100	1	0	0	0	0	0	0	0
CAF-076	Incertae sedis	CAF-076	0	0	0	1	0	0	0	0
CAF-103	Incertae sedis	CAF-103	0	0	0	1	0	0	0	0
CAF-104	Incertae sedis	CAF-104	0	1	1	0	0	0	0	0
CAF-130	Incertae sedis	CAF-130	0	0	0	0	0	1	0	0

Morph Number	Family	Taxa	Stenkul Fiord Area	Split Lake	Strand Fiord	Strathcona Fiord	Fosheim South	Fosheim North	Judge Daly Promontory	Lake Hazen
CAF-132	Incertae sedis	CAF-132	0	0	0	0	1	0	0	0
CAF-134	Incertae sedis	CAF-134	1	0	0	0	0	0	0	0
CAF-151	Incertae sedis	CAF-151	0	0	1	0	0	0	0	0
CAF-086	Incertae sedis	CAF-086	1	1	0	0	1	1	1	0
CAF-123	Incertae sedis	CAF-123	1	0	0	0	0	0	0	0
CAF-124	Incertae sedis	CAF-124	0	0	0	0	1	0	0	0
CAF-137	Incertae sedis	CAF-137	1	0	0	0	0	0	0	0
CAF-146	Incertae sedis	CAF-146	0	0	0	0	1	0	0	0
CAF-147	Incertae sedis	CAF-147	0	0	0	0	0	0	0	1
CAF-093	Incertae sedis	CAF-093	0	0	0	0	0	0	0	1
CAF-138	Incertae sedis	CAF-138	0	0	0	0	0	1	0	0
CAF-142	Incertae sedis	CAF-142	1	0	0	0	0	0	0	0
CAF-143	Incertae sedis	CAF-143	0	0	1	0	0	0	0	0
CAF-145	Incertae sedis	CAF-145	0	0	0	0	1	0	0	0
CAF-140	Incertae sedis	CAF-140	1	0	0	0	0	0	0	0
CAF-141	Incertae sedis	CAF-141	1	0	0	0	0	0	0	0

Table 3.1: Table of the major locality zones and fossil megaflora morphotypes found there. Data presented as presence and absence. 1 = present, 0 = absent.

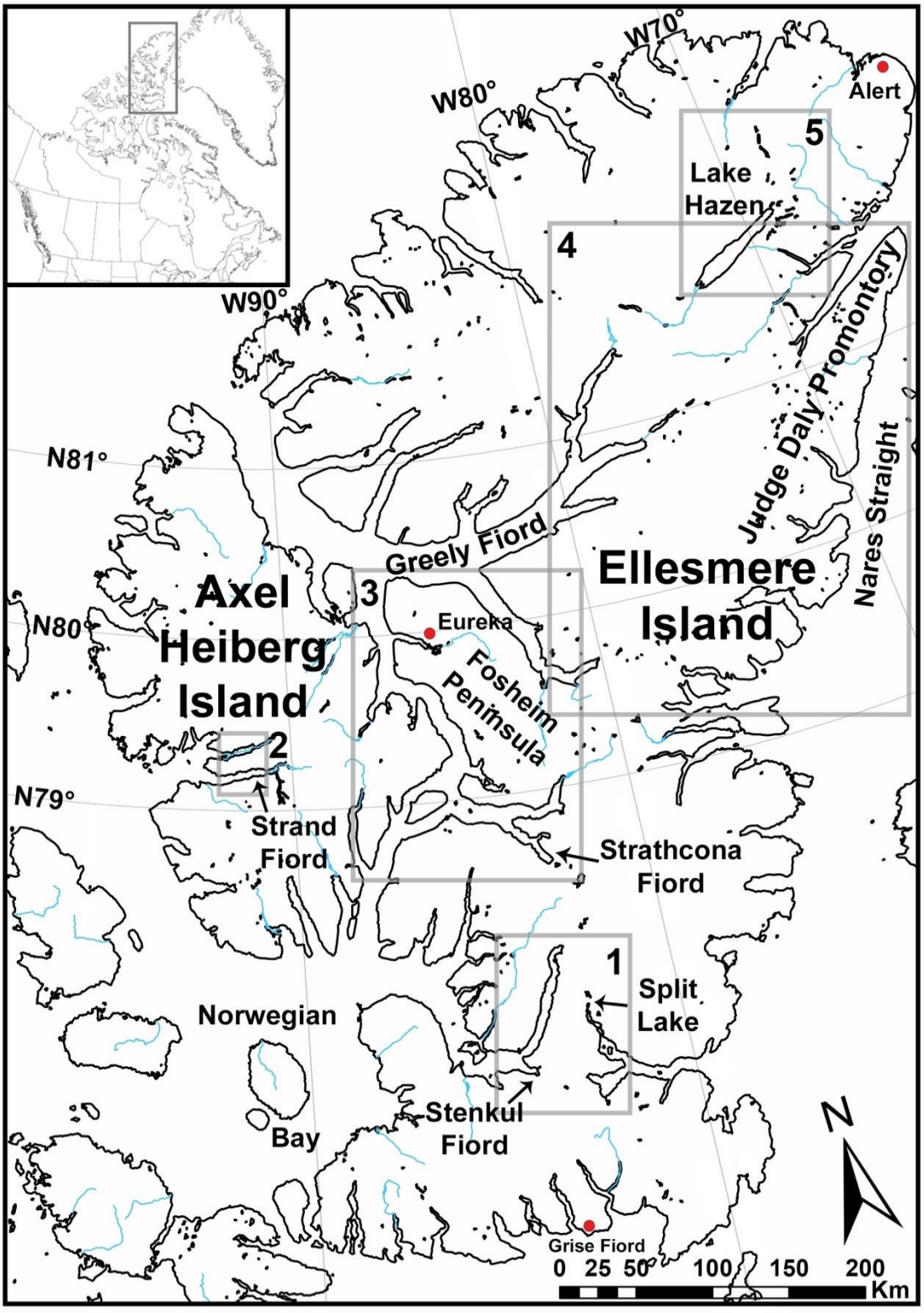

Figure 3.1: Location map showing position of Ellesmere and Axel Heiberg islands. Boxes 1-5 correspond to geologic maps (Figures 3.3-3.8) of fossil localities.

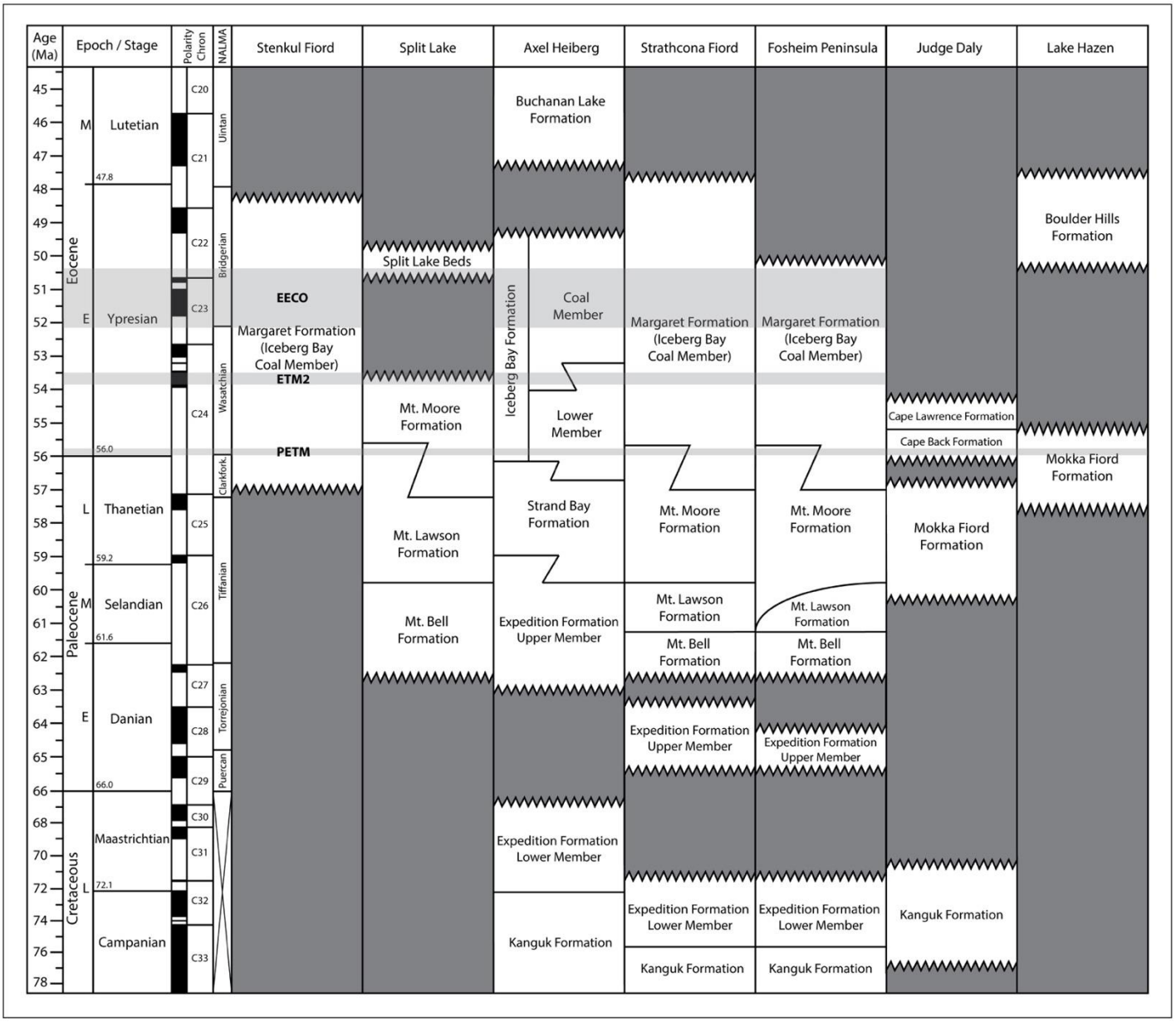

Figure 3.2: Generalized stratigraphy on Ellesmere and Axel Heiberg islands. Formations belonging to the Eureka Sound Group include those developed by MIALL (1986): Mount Bell, Vesle Fiord, Mount Lawson, Mount Moore, Cape Back, Cape Lawrence, Mokka Fiord, Margaret, and Boulder Hills formations. The formations developed by RICKETTS (1986) include: the Expedition, Strand Bay, Iceberg Bay, and the Buchanana Lake formations. Compiled from HARRISON et al. 1999; REINHARDT et al. 2013; WEST et al. 2015.

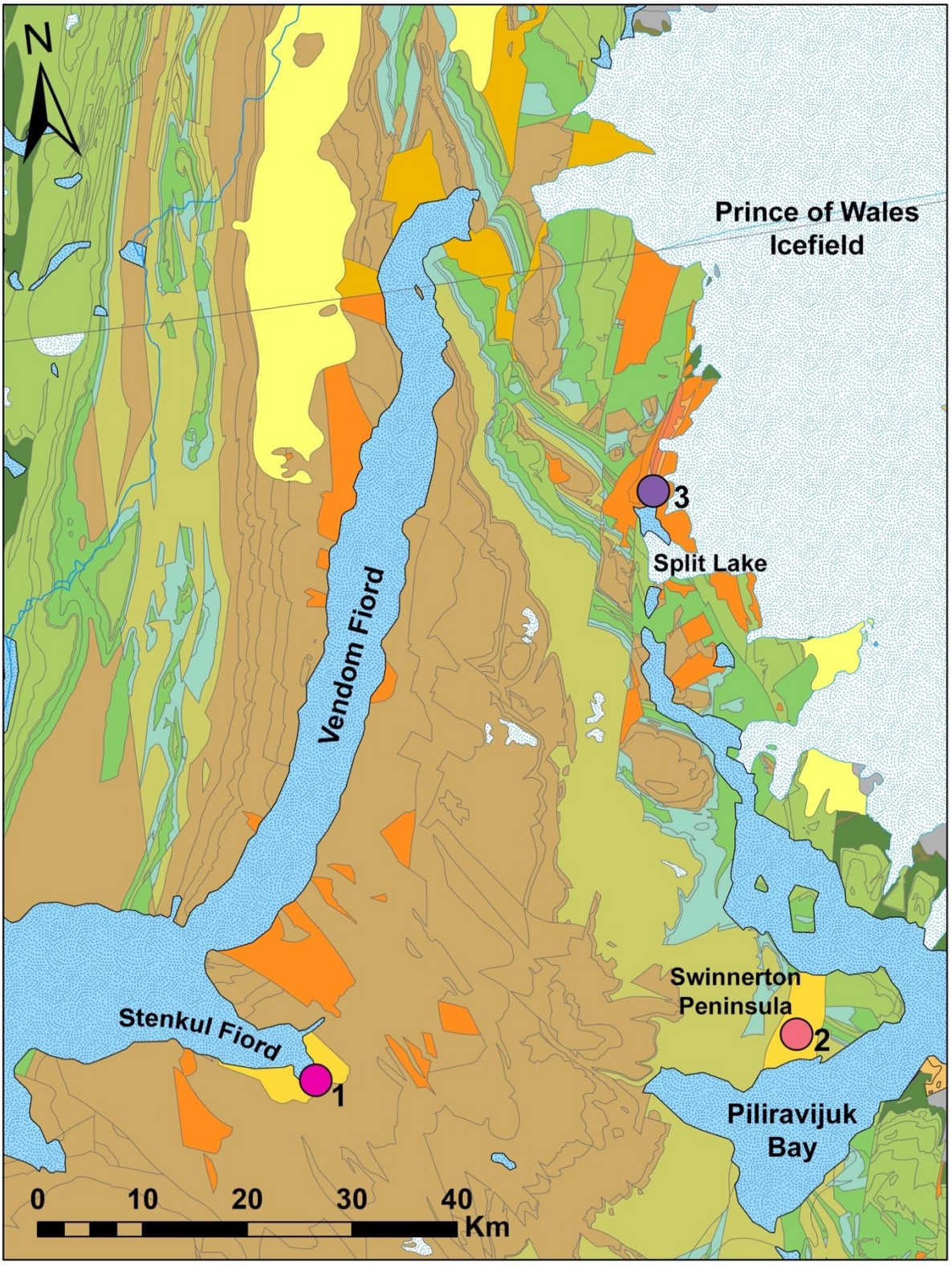

Figure 3.3: Simplified geological map of the local geology for the Stenkul Fiord and Split Lake areas, Ellesmere Island. Corresponds to box 1 on figure 3.1. Modified from HARRISON et al. 2016. Dot 1 represents localities USPC 430-439, 1005, 1012, 1014; YPM 7973, 8410-8418, 8426, 848. Dot 2 represents localities YPM 8422, 8545, 8547. Dot 3 represents localities USPC 441-444.

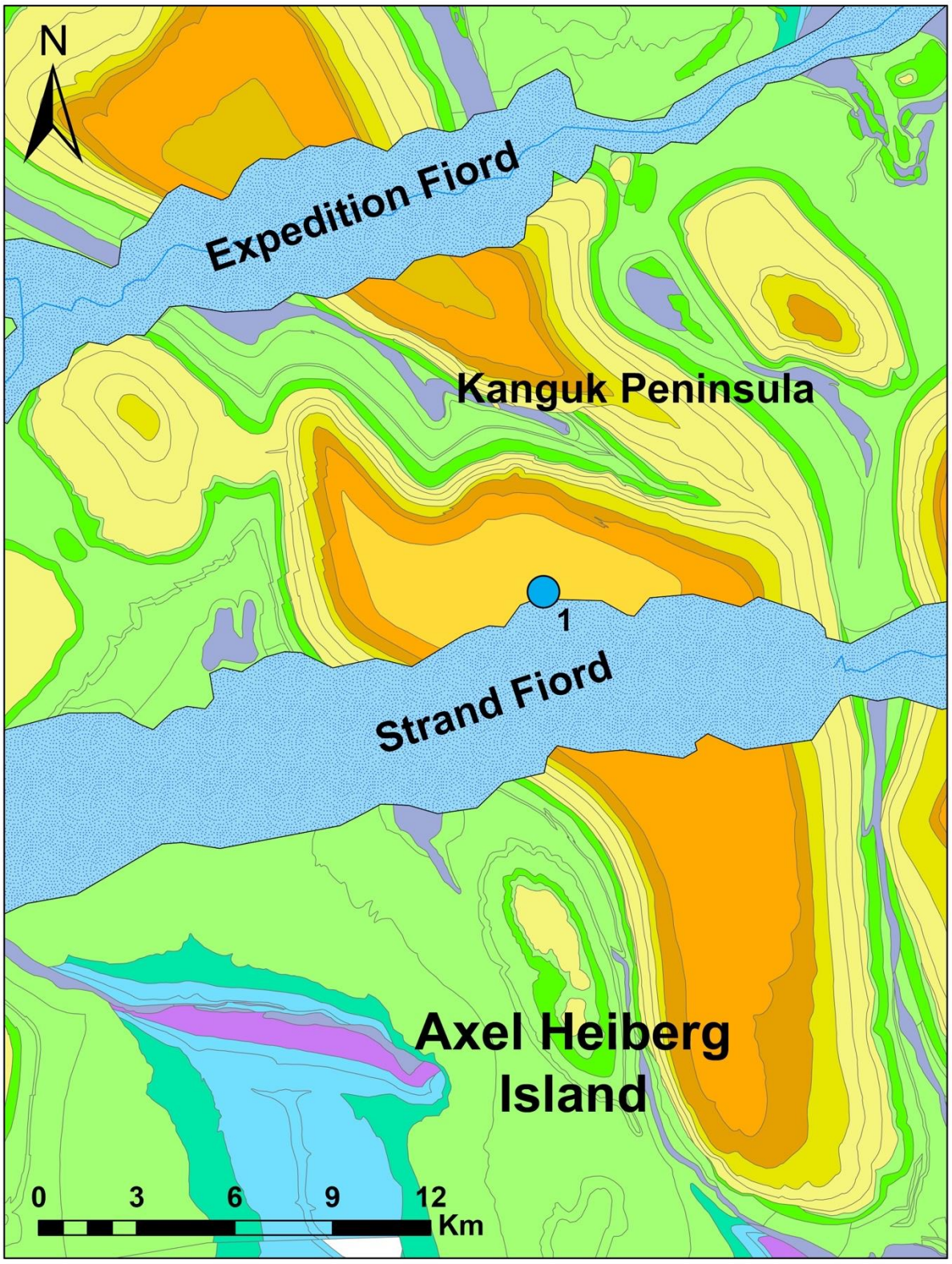

Figure 3.4: Simplified geological map of the local geology for Strand Fiord, Axel Heiberg Island. Corresponds to box 2 on figure 3.1. Modified from HARRISON et al. 2016. Dot 1 represents localities USPC 162-179, and YPM 7920.

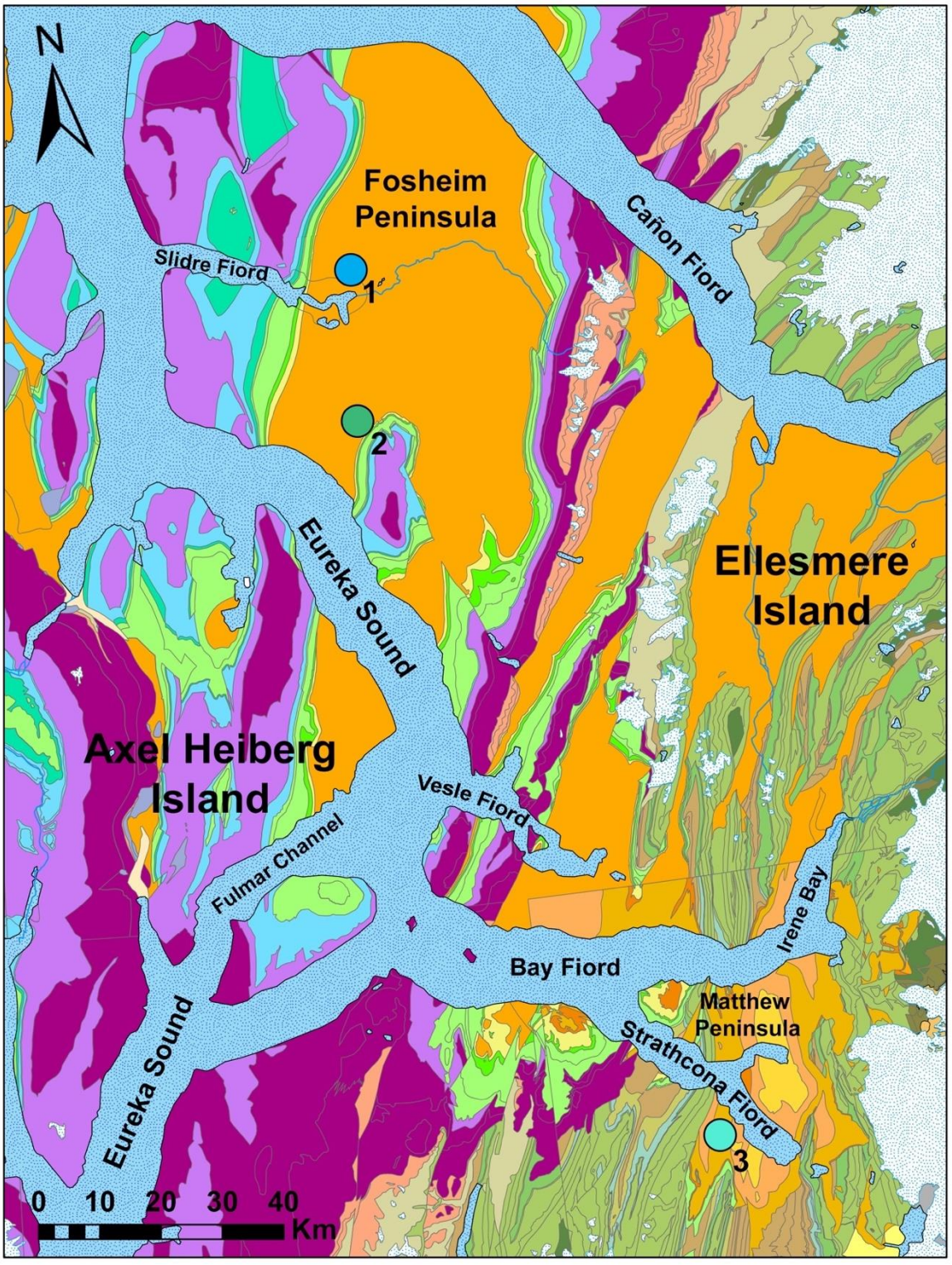

Figure 3.5: Simplified geological map of the local geology of the Fosheim Peninsula and Strathcona Fiord areas, Ellesmere Island. Corresponds to box 3 on figure 3.1. Modified from HARISSON et al. 2016. Dot 1 represents localities USPC 6, 100-102, 104, 105, 108, 191, 193, 195-200, 657, 661; YPM 7936, 7937, 8432. Dot 2 represents localities USPC 22, 23-26, 111, 250, 251, 253, 259. Dot 3 represents localities USPC 358-371, 411 and includes localities from Bay Fiord YPM 7950, 7962, 7969, 7971, 8437, 8441, and Matthew Peninsula YPM 8518.

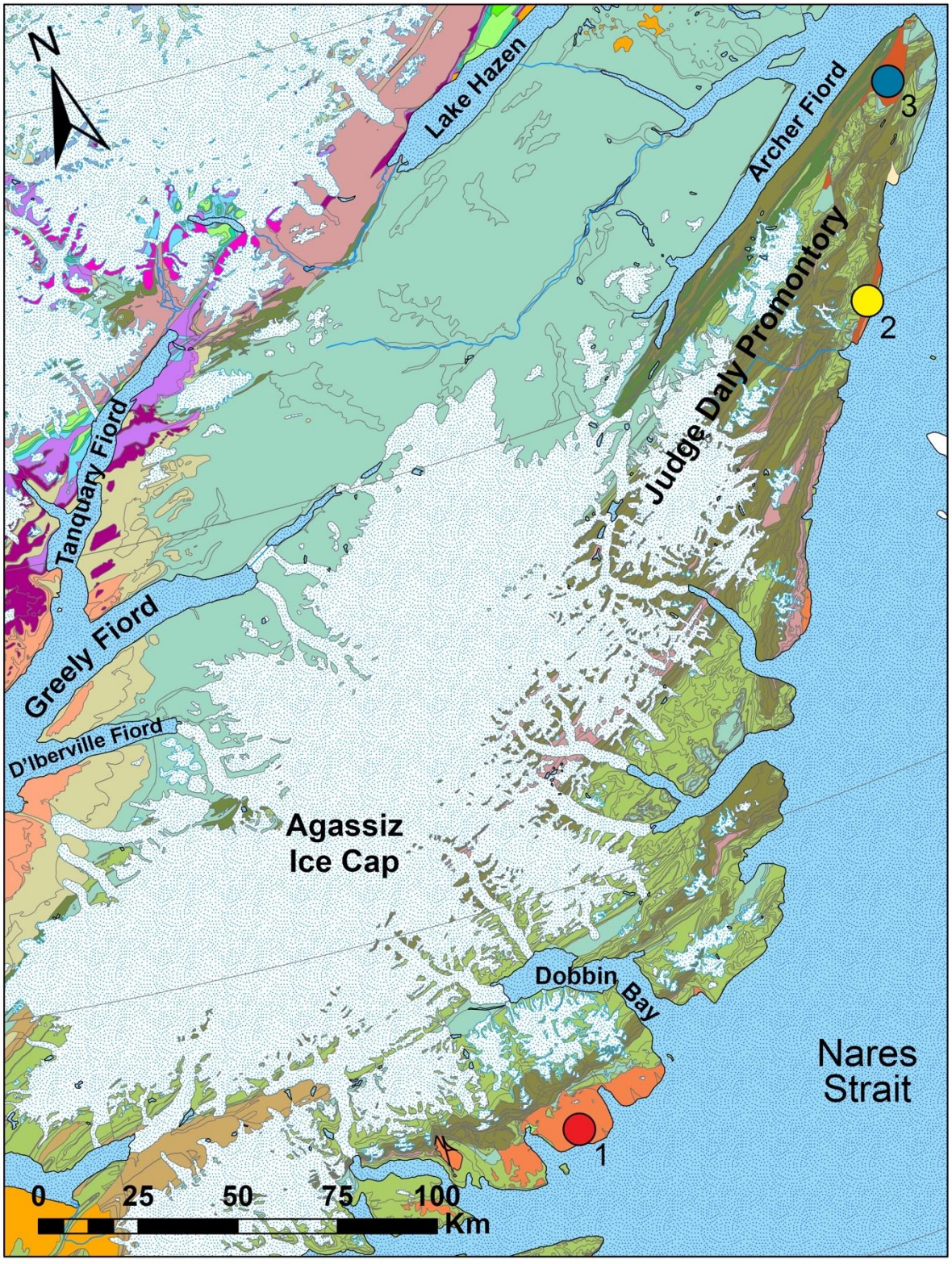

Figure 3.6: Simplified geological map of the local geology for the Judge Daly Promontory, Ellesmere Island. Corresponds to box 4 on figure 3.1. Modified from HARRISON et al. 2016. Dot 1 represents localities USPC 716 and 718. Dot 2 represents localities USPC 708, 710-712, 715. Dot 3 represents localities USPC 752-759.

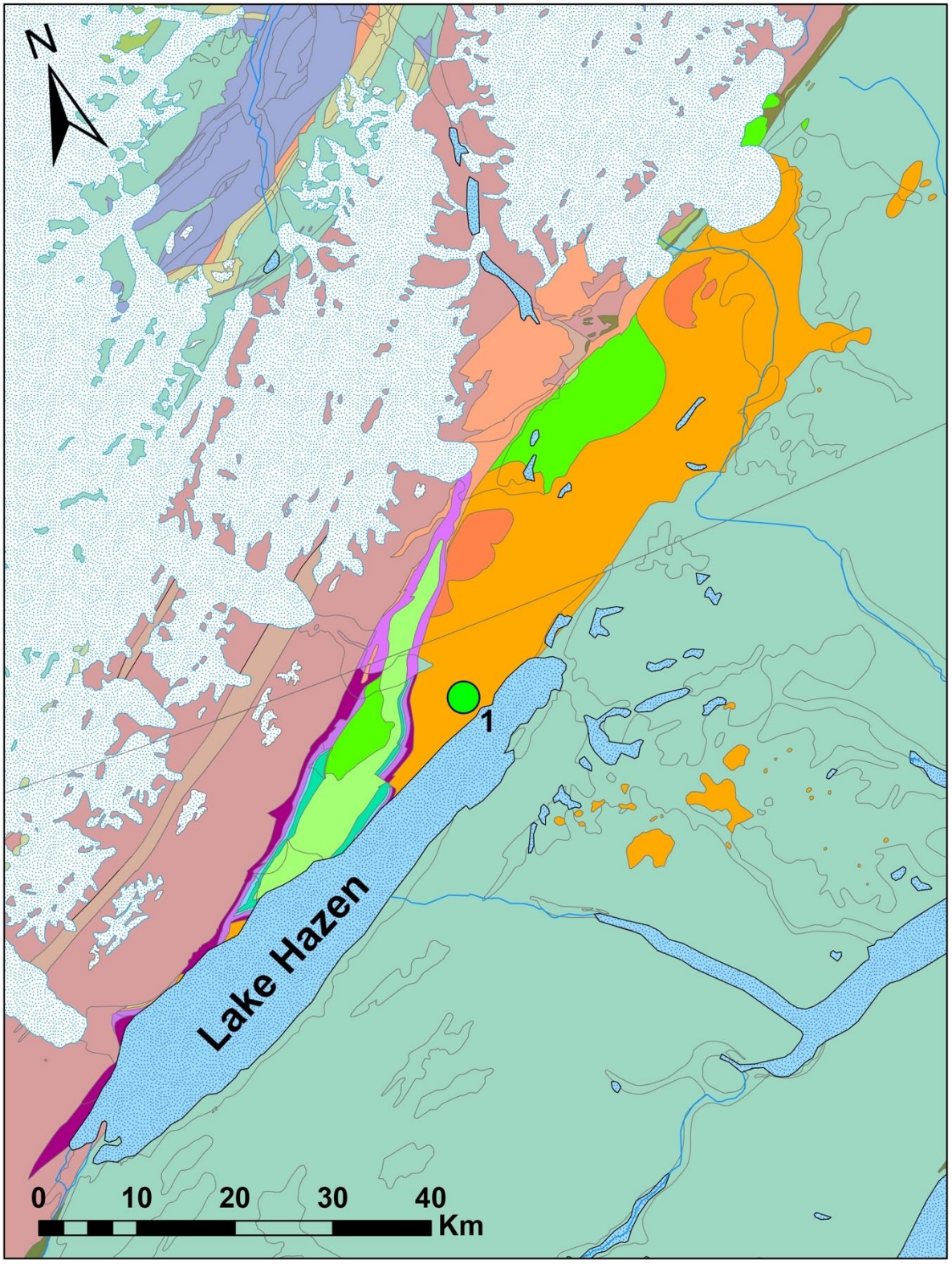

Figure 3.7: Simplified geological map of the local geology for Lake Hazen, Ellesmere Island. Corresponds to box 5 on figure 3.1. Modified from HARRISON et al. 2016. Dot 1 represents localities USPC 261, 267, 268, 275.

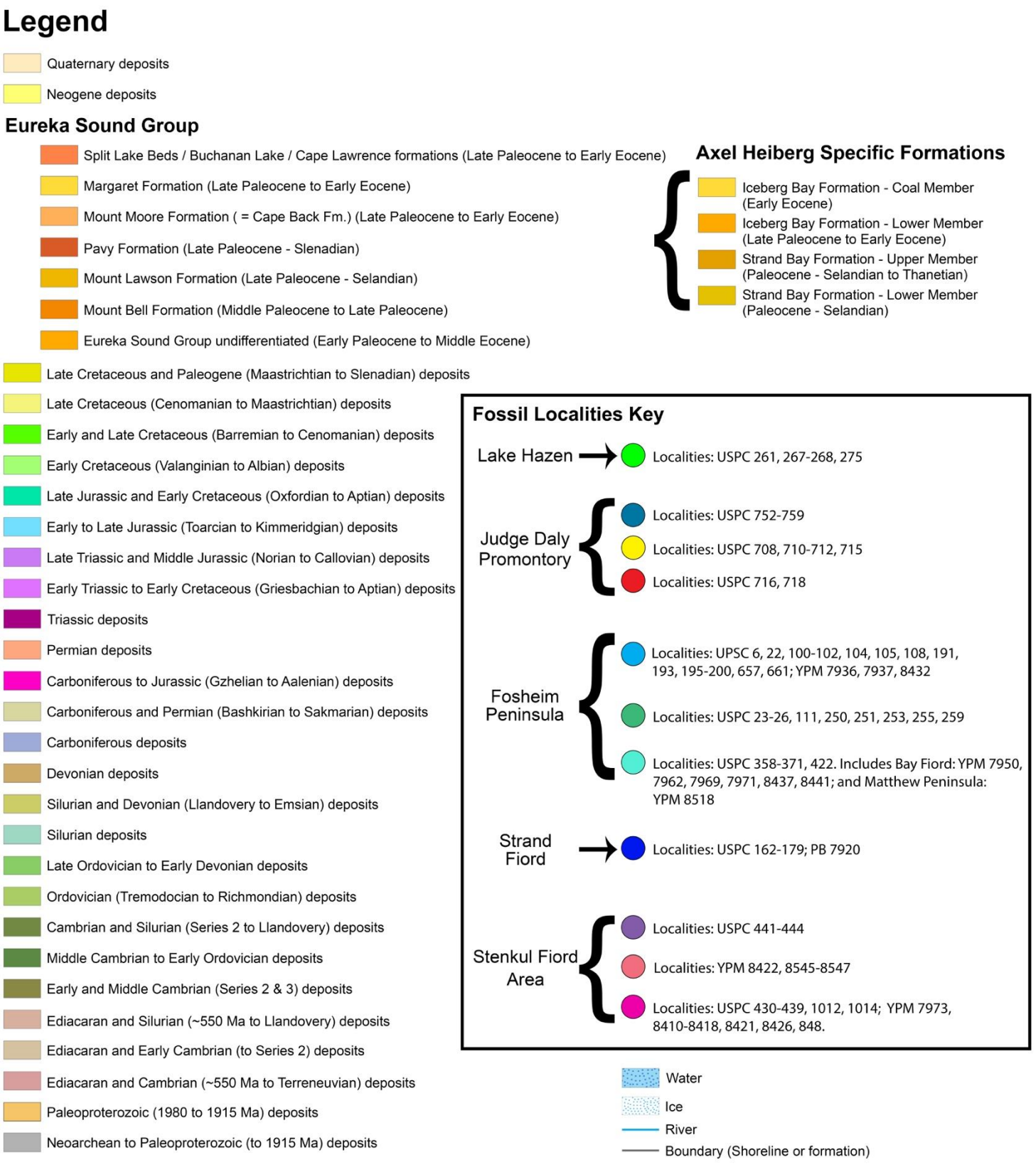

Figure 3.8: Master legend of geological formations from Ellesmere and Axel Heiberg islands and locality key for figures 3.3-3.7.

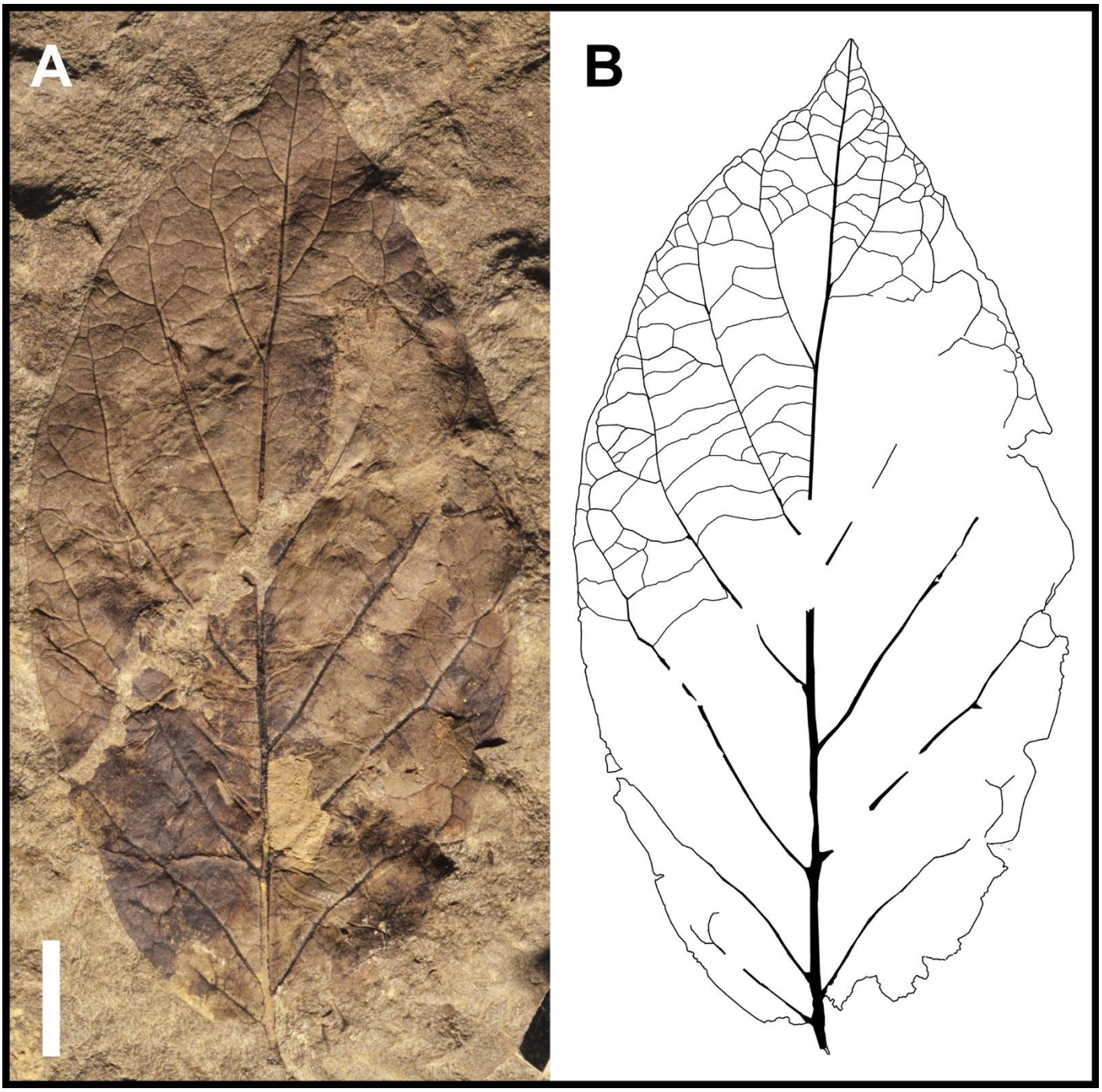

Figure 3.9: Morphotype exemplar of CAF-102, cf. *Magnolia* sp. A, USPC 111-4885. B, Line drawing of the morphotype exemplar. Scale 1 cm.

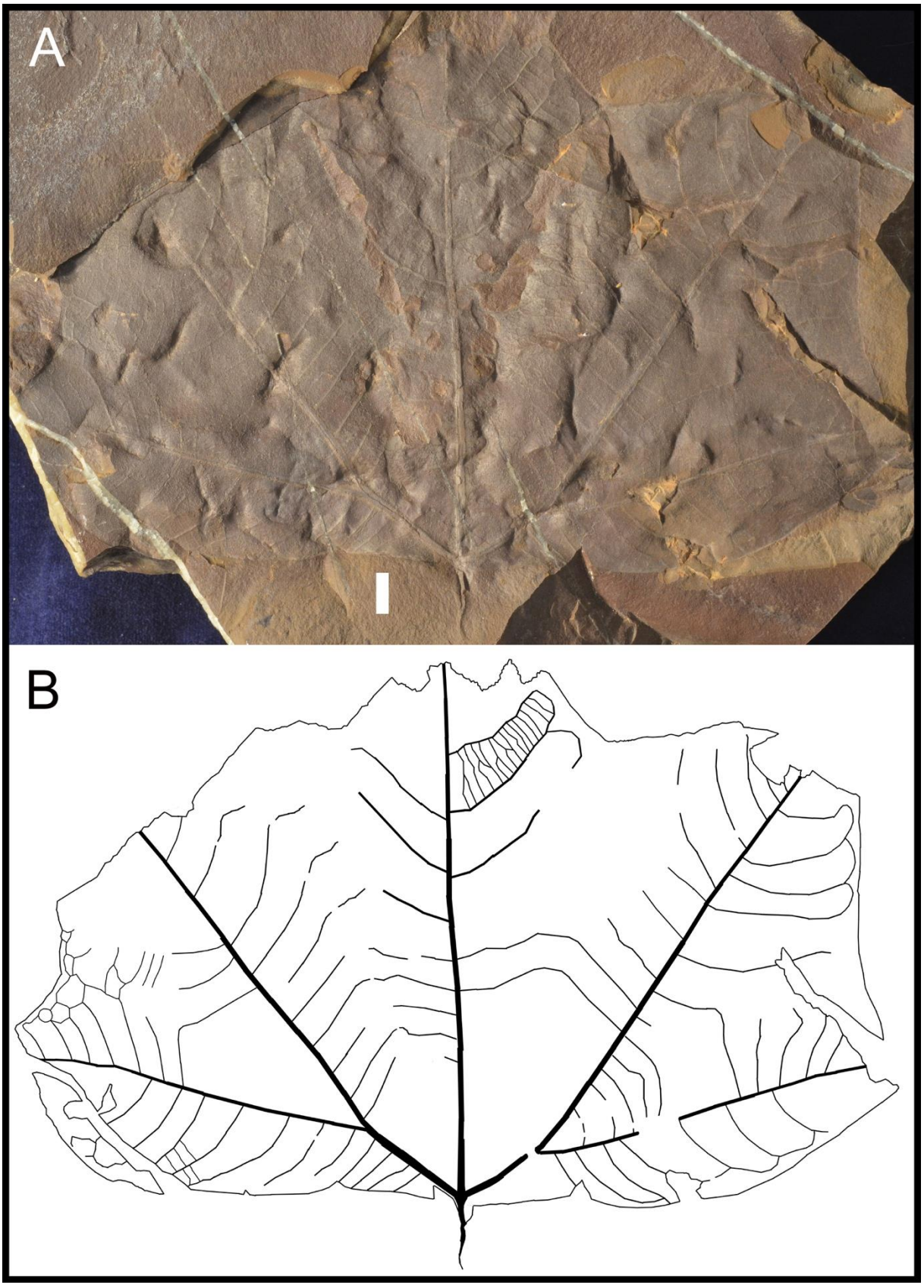

Figure 3.10: Morphotype exemplar of CAF-080, *Macginitiea* aff. *M. nobilis* (NEWBERRY) MANCHESTER. A, YPM PB 169818. B, line drawing of the morphotype exemplar. Scale 1 cm.

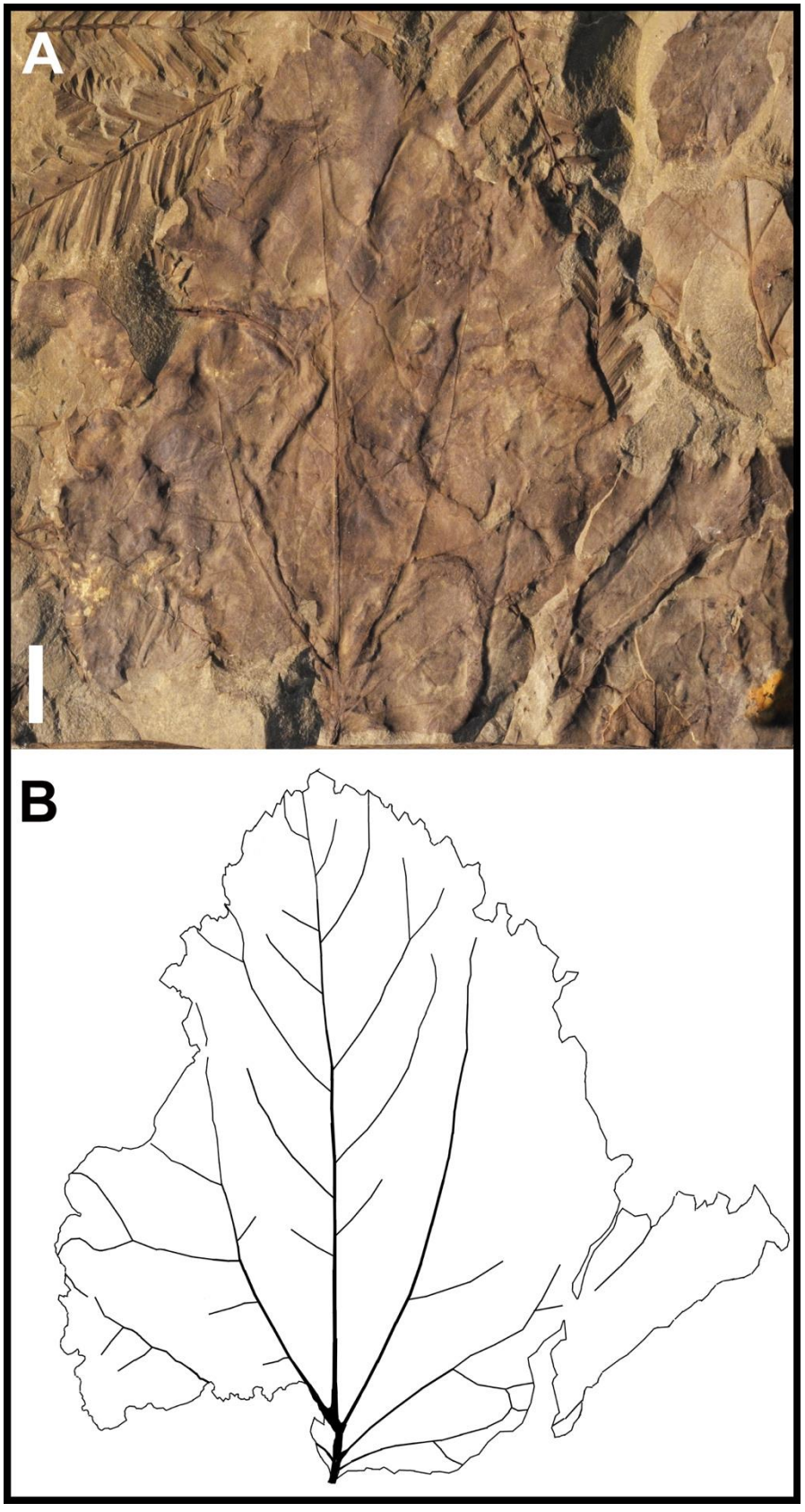

Figure 3.11: Morphotype exemplar of CAF-128, *Platanus* sp. A, USPC 111-4879. B, line drawing of the morphotype exemplar. Scale 1 cm.

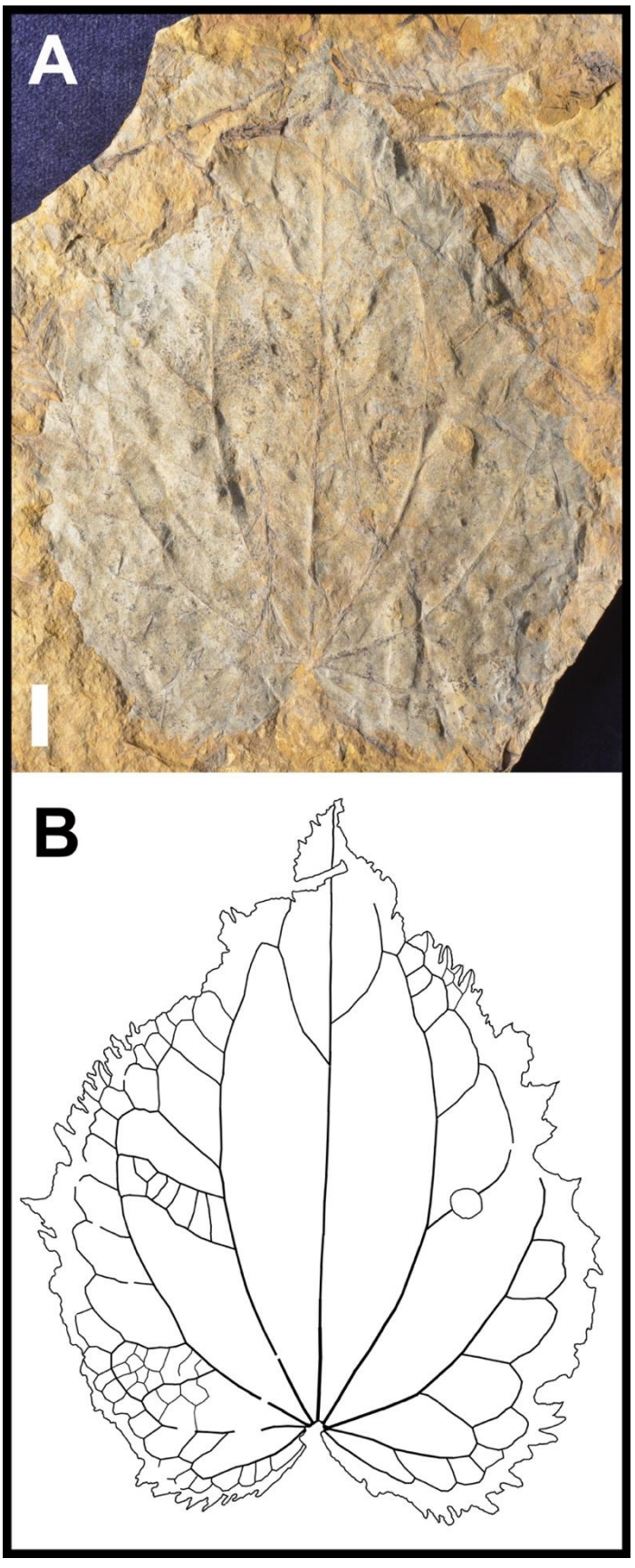

Figure 3.12: Morphotype exemplar of CAF-040, *Tetracentron* cf. *T. hopkinsii* PIGG, DILLHOFF, DEVORE et WEHR. Previously figured in WEST et al. 2015, figure 5 as STF004. A, USPC 422-

3871. B, line drawing of the morphotype exemplar. Scale 1 cm.

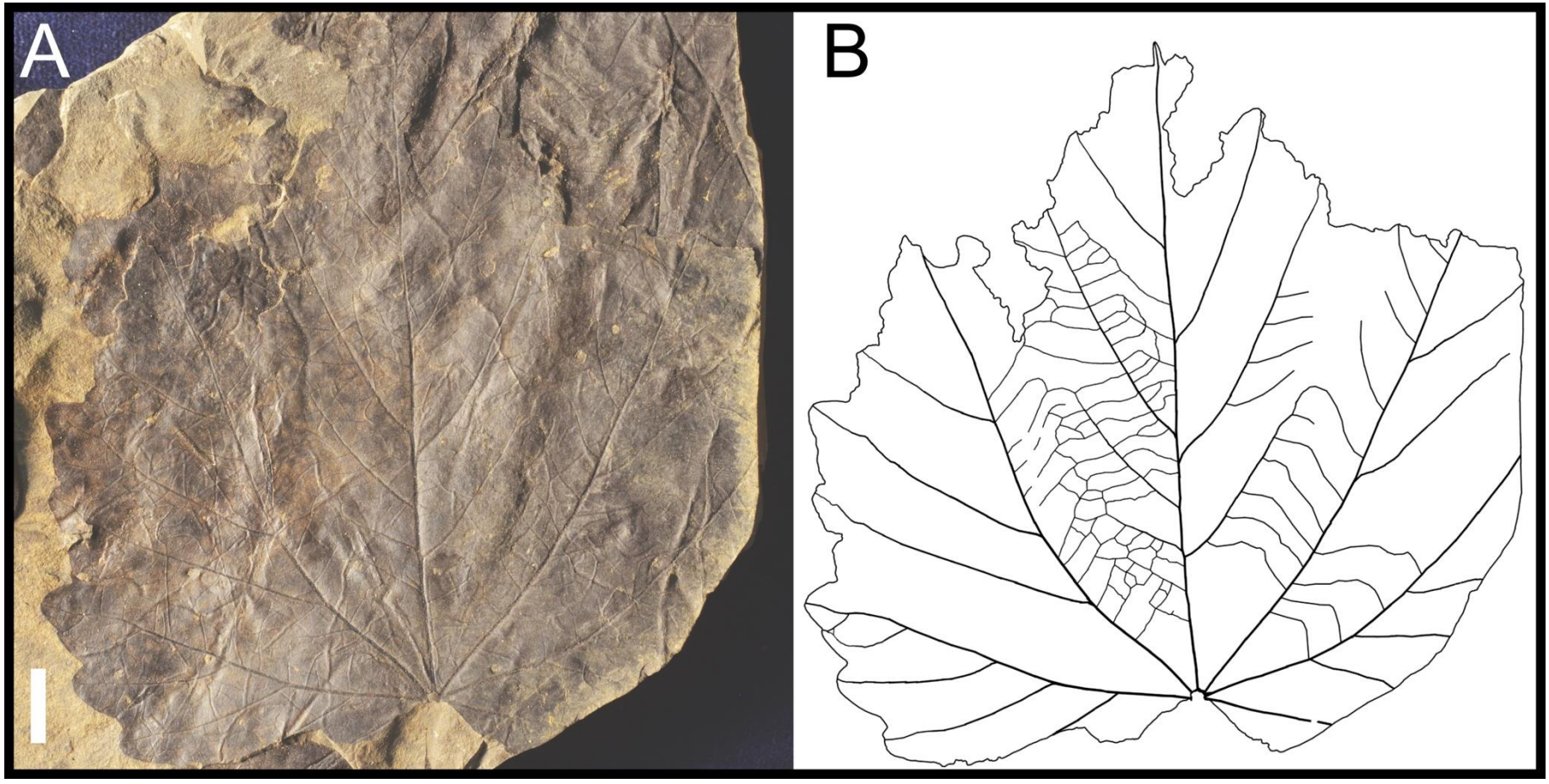

Figure 3.13: Morphotype exemplar of CAF-034, *Archeampelos* cf. *A. acerifolia* (NEWBERRY) MCIVER et BASINGER. Previously figured in WEST et al. 2015, figure 3 as SF023. A, USPC 436-2732.2. B, line drawing of the morphotype exemplar. Scale 1 cm.

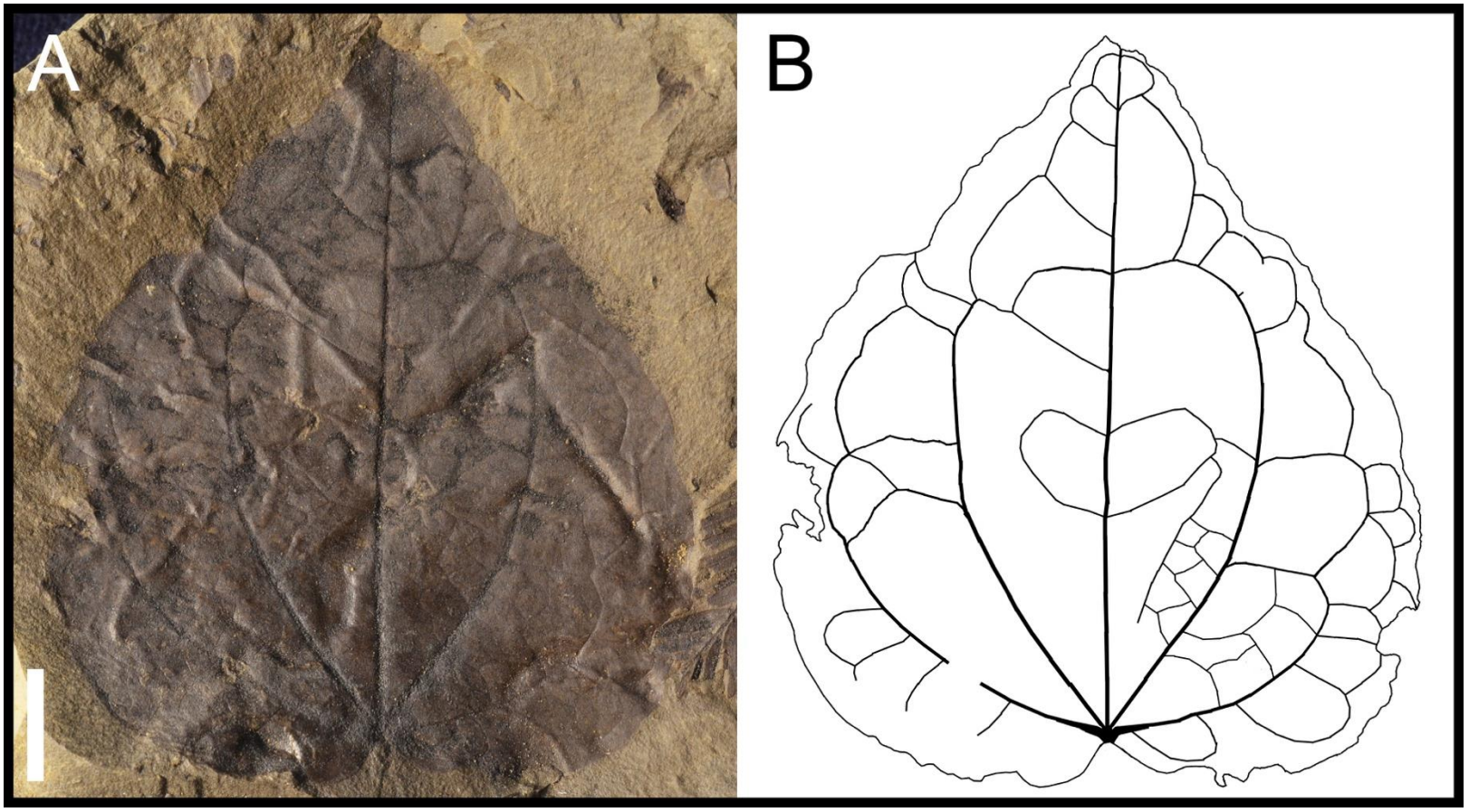

Figure 3.14: Morphotype exemplar of CAF-035, *Trochodendroides arctica* (HEER) BERRY. Previously figured in WEST et al. 2015, figure 3 as SF024. A, USPC 439-2809.2. B, line drawing of the morphotype exemplar. Scale 1 cm.

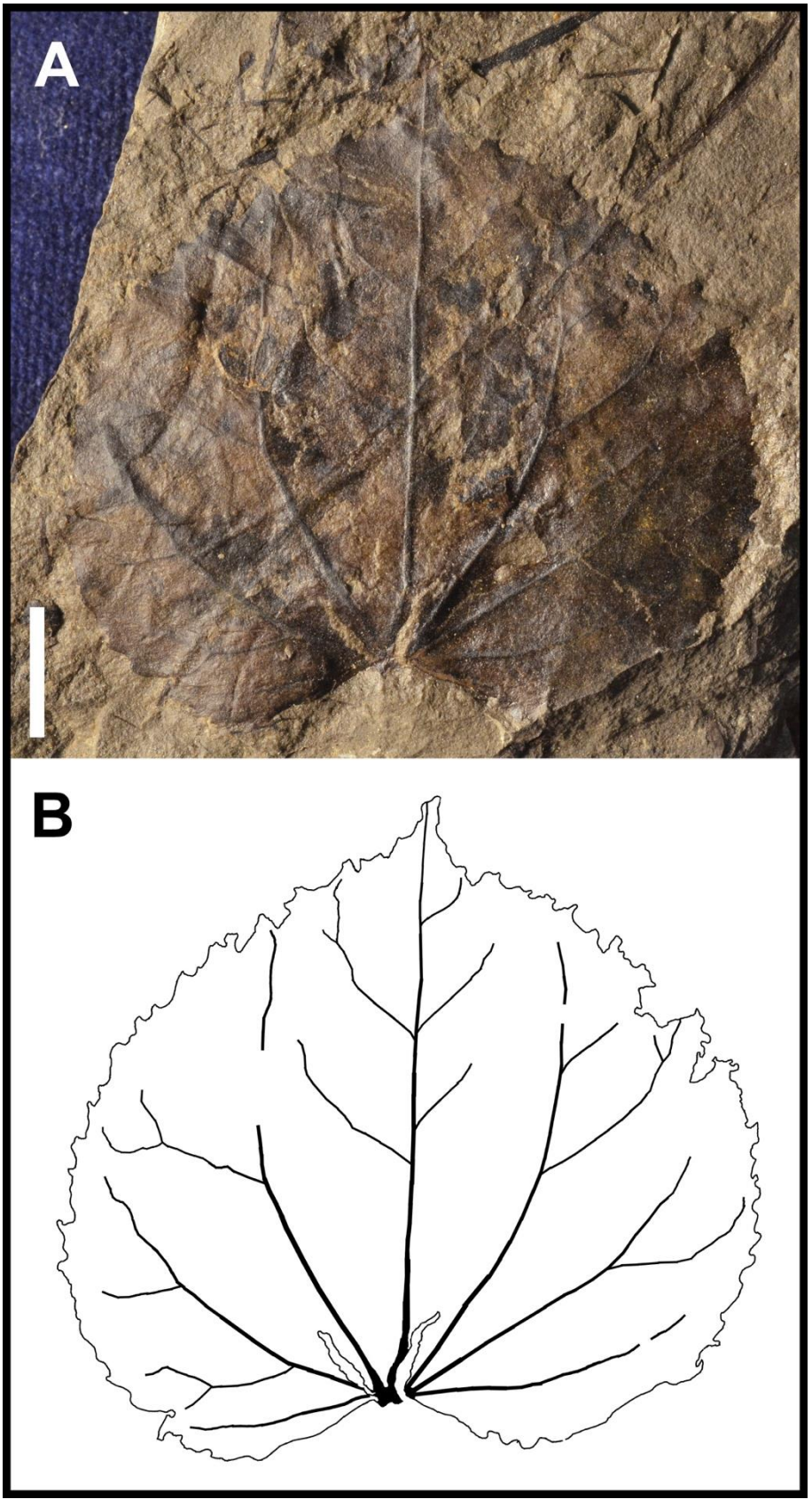
A
B

Figure 3.15: Morphotype exemplar of CAF-036, *Trochodendroides curvidens* (HEER) GOLOVNEVA et BUDANTSEV. Previously figured in WEST et al. 2015, figure 3 as SF025. A, USPC 436-2750. B, line drawing of the morphotype exemplar. Scale 1 cm.

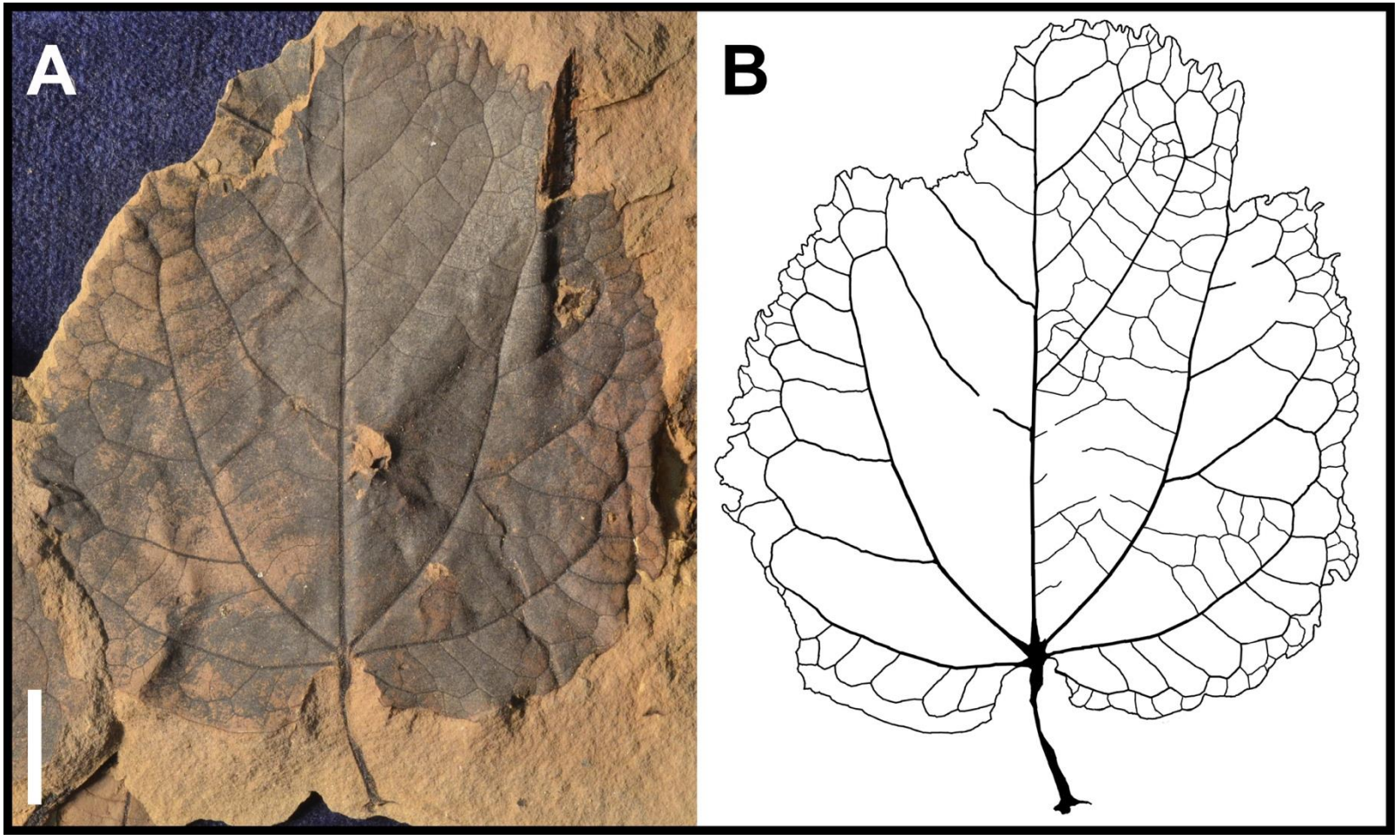

Figure 3.16: Morphotype exemplar of CAF-021, *Trochodendroides crenulata* (HEER) KVAČEK, MANUM et BOULTER. Previously figured in WEST et al. 2015, figure 3 as SF010. A, USPC 435-2706.1. B, line drawing of the morphotype exemplar. Scale 1 cm.

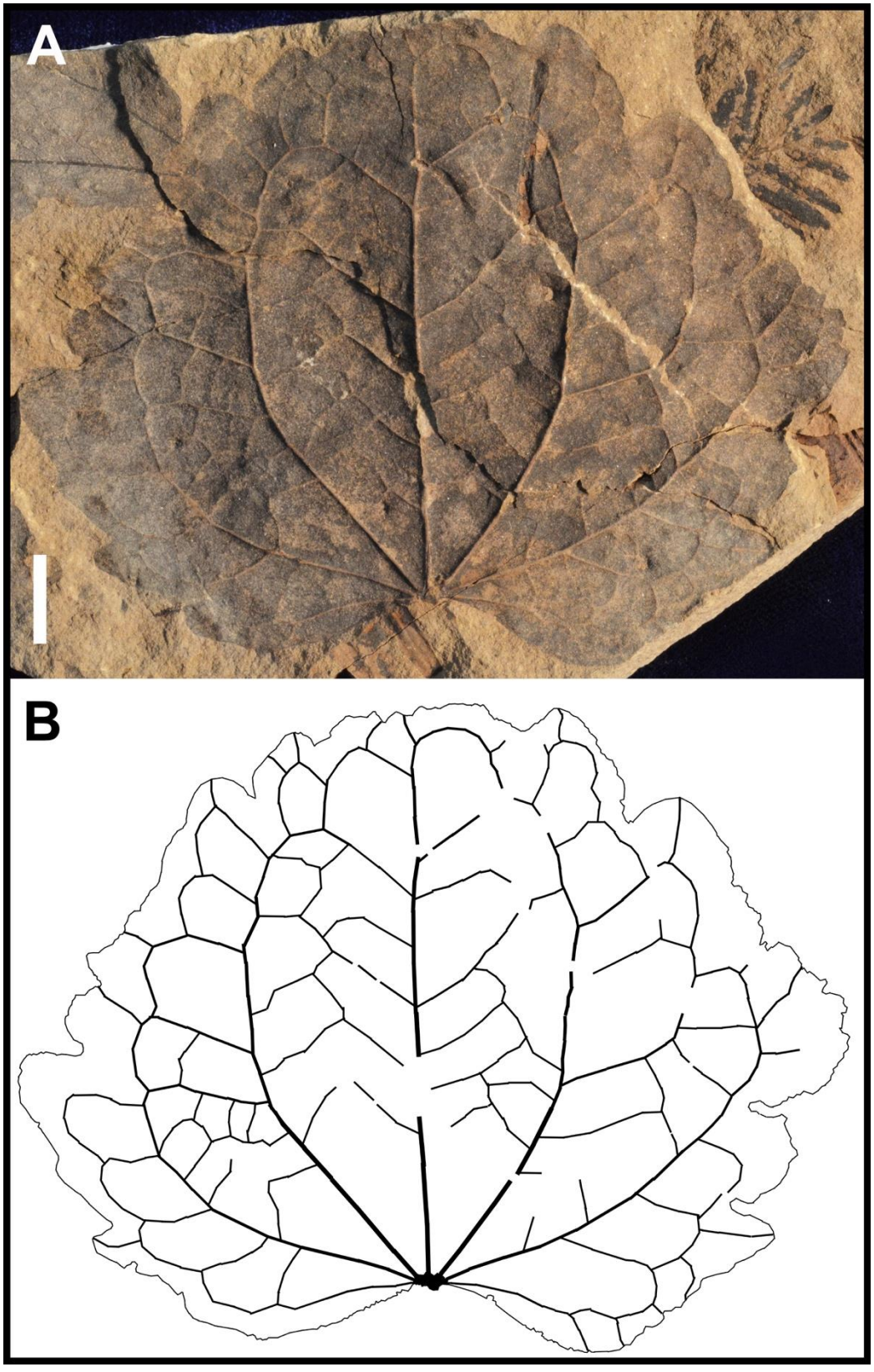

Figure 3.17: Morphotype exemplar of CAF-098, *Trochodendroides richardsonii* (HEER) KRYSHTOFOVICH. Previously figured in MCIVER & BASINGER 1999, figure 14. A, USPC 435-2696. B, line drawing of the morphotype exemplar. Scale 1 cm.

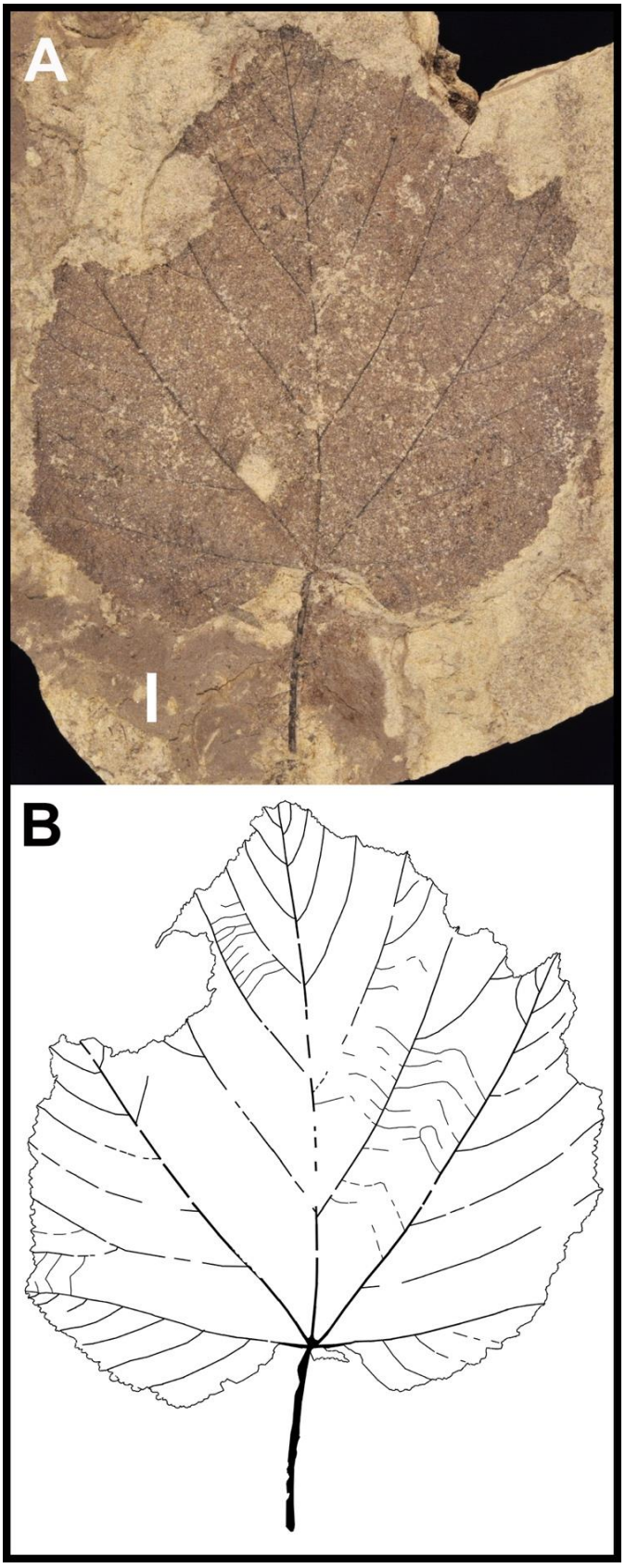

Figure 3.18: Morphotype exemplar of CAF-004, *Vitiphyllum* cf. *V. sewardii* BOULTER et KVAČEK. Previously figured in WEST et al. 2015, figure 4 as SL004. A, USPC 442-2820. B, line drawing of the morphotype exemplar. Scale 1 cm.

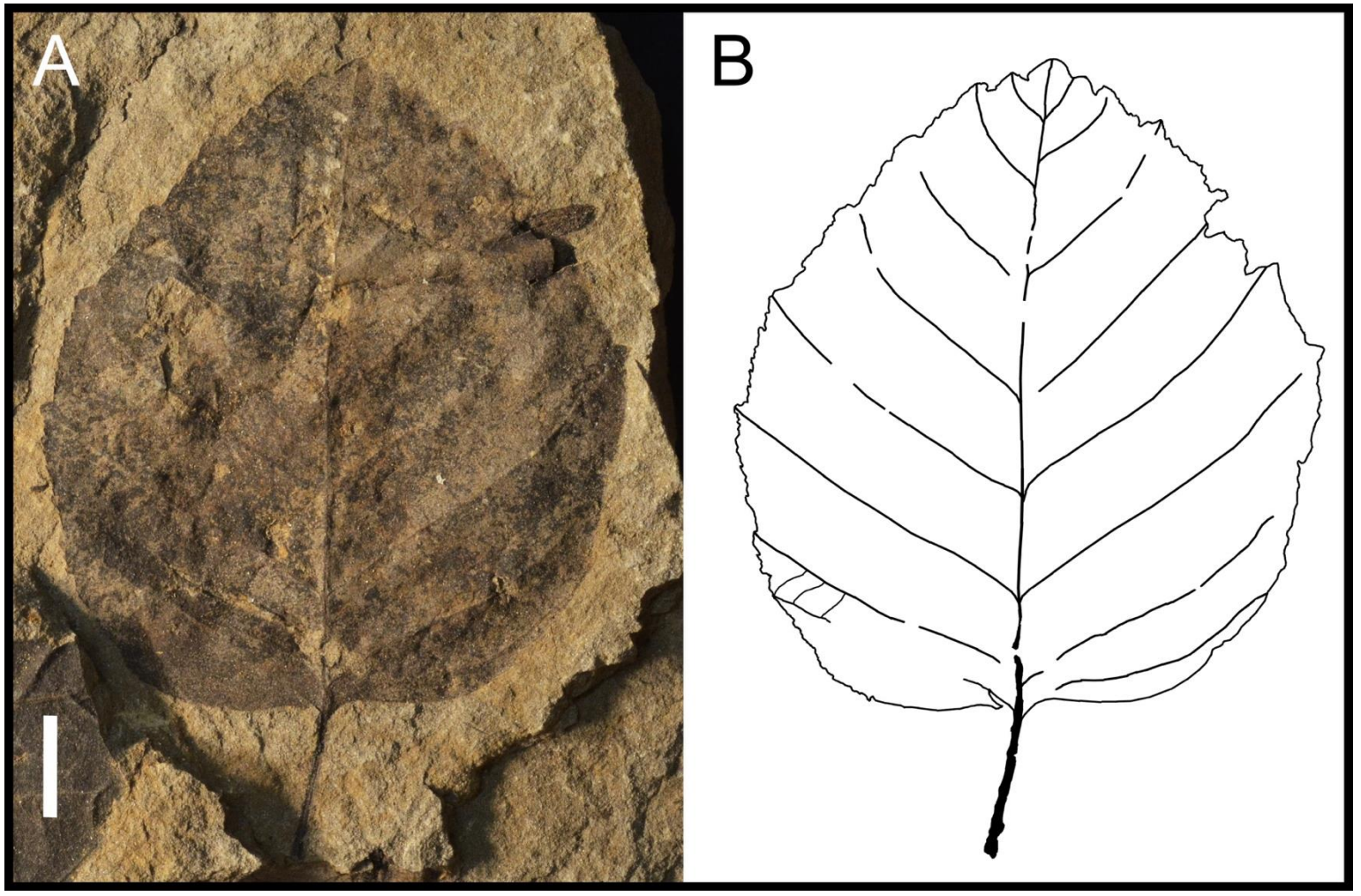

Figure 3.19: Morphotype exemplar of CAF-061, *Alnus* cf. *A. parvifolia* (BERRY) WOLFE et WEHR. A, USPC 267-6353. B, line drawing of the morphotype exemplar. Scale 1 cm.

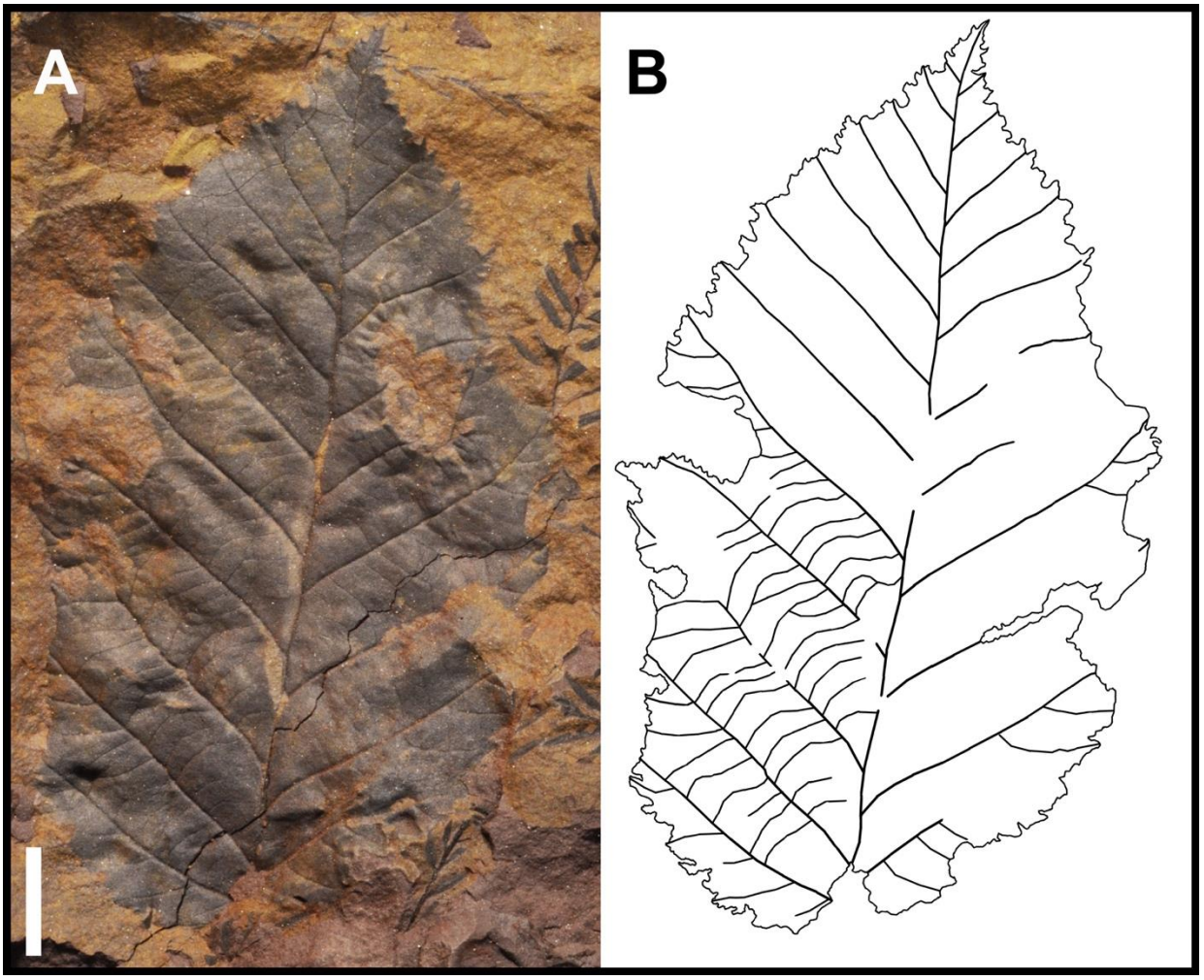

Figure 3.20: Morphotype exemplar of CAF-031, cf. *Paracarpinus* sp. A, USPC 22-1143. B, line drawing of the morphotype exemplar. Scale 1 cm.

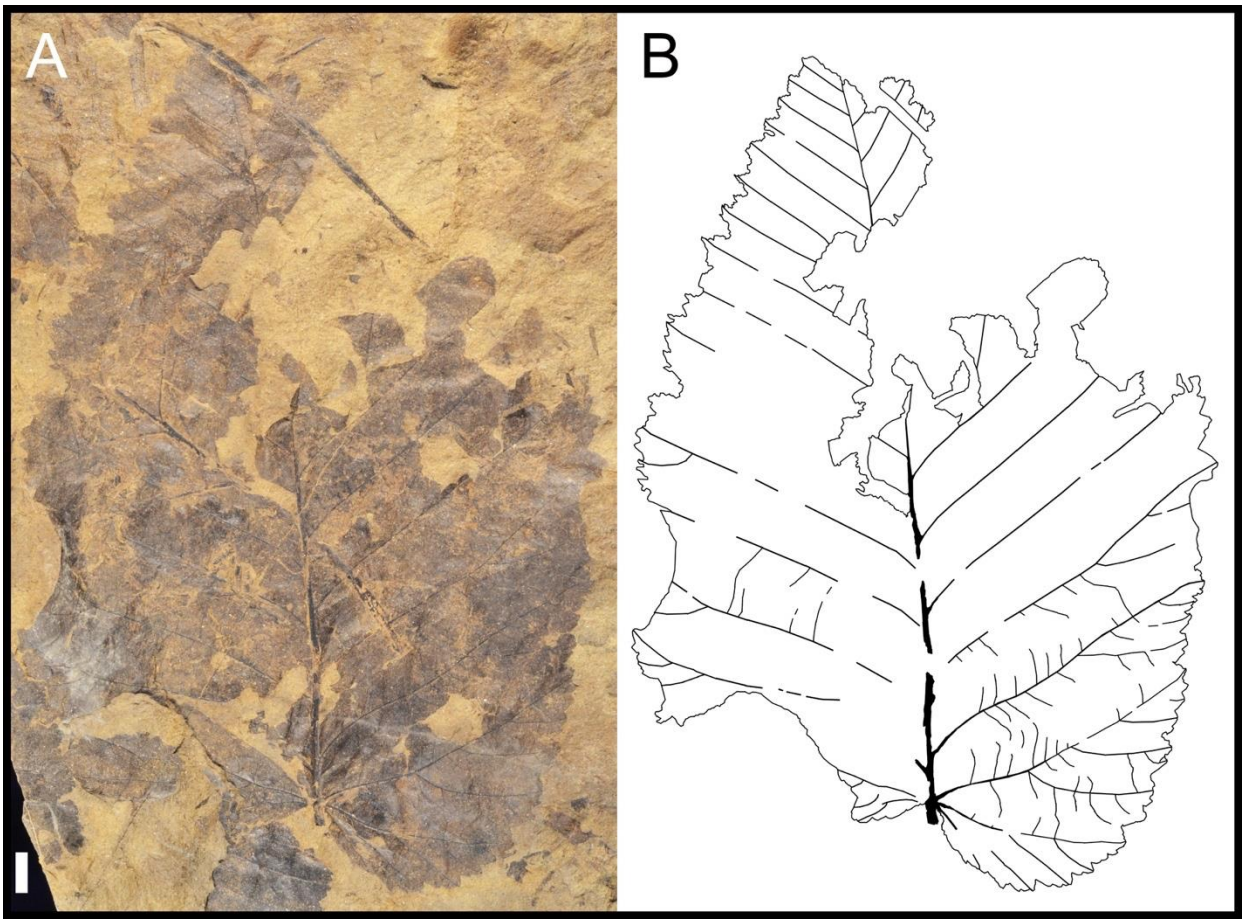

Figure 3.21: Morphotype exemplar of CAF-129, *Corylites hebridicus* SEWARD et HOLTTUM. A, USPC 367-3896. B, line drawing of the morphotype exemplar. Scale 1 cm.

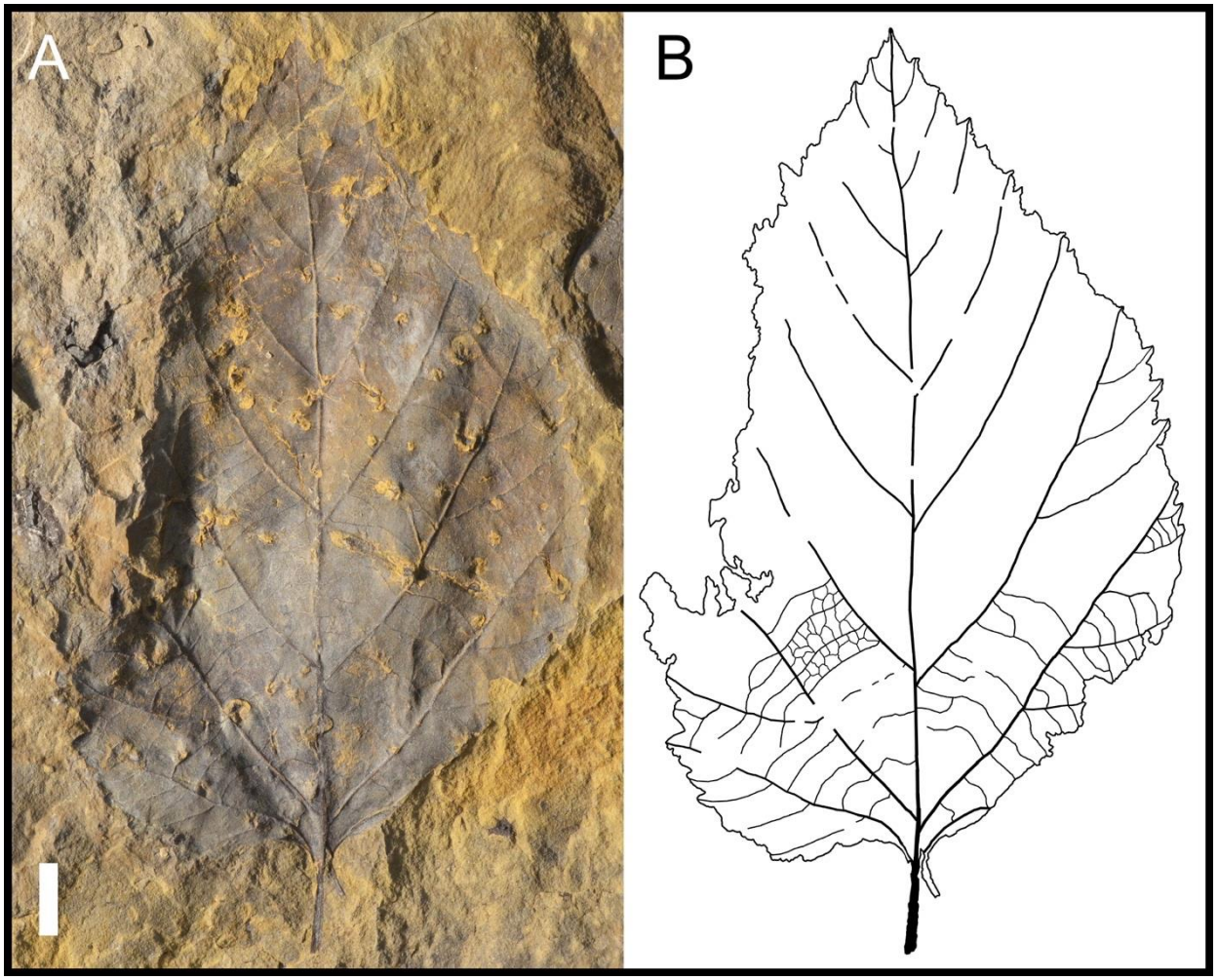

Figure 3.22: Morphotype exemplar of CAF-054, *Craspedodromophyllum* cf. *C. malmgrenii* (HEER) GOLOVNEVA. A, USPC 200-4777. B, line drawing of the morphotype exemplar. Scale 1 cm.

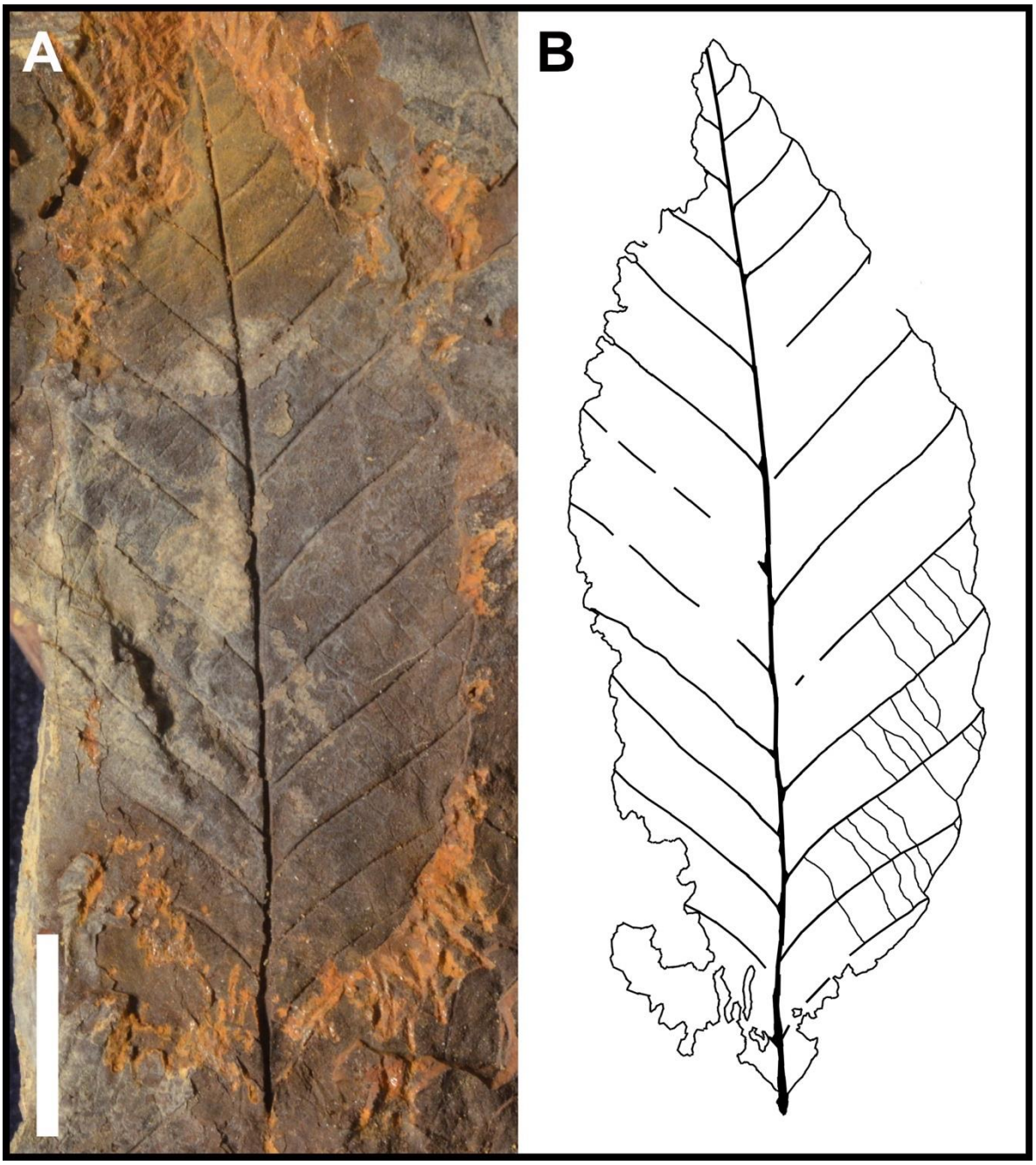

Figure 3.23: Morphotype exemplar of CAF-065, *Fagopsiphyllum* cf. *F. groenlandicum* (HEER) MANCHESTER. A, YPM PB 169838. B, line drawing of the morphotype exemplar. Scale 1 cm.

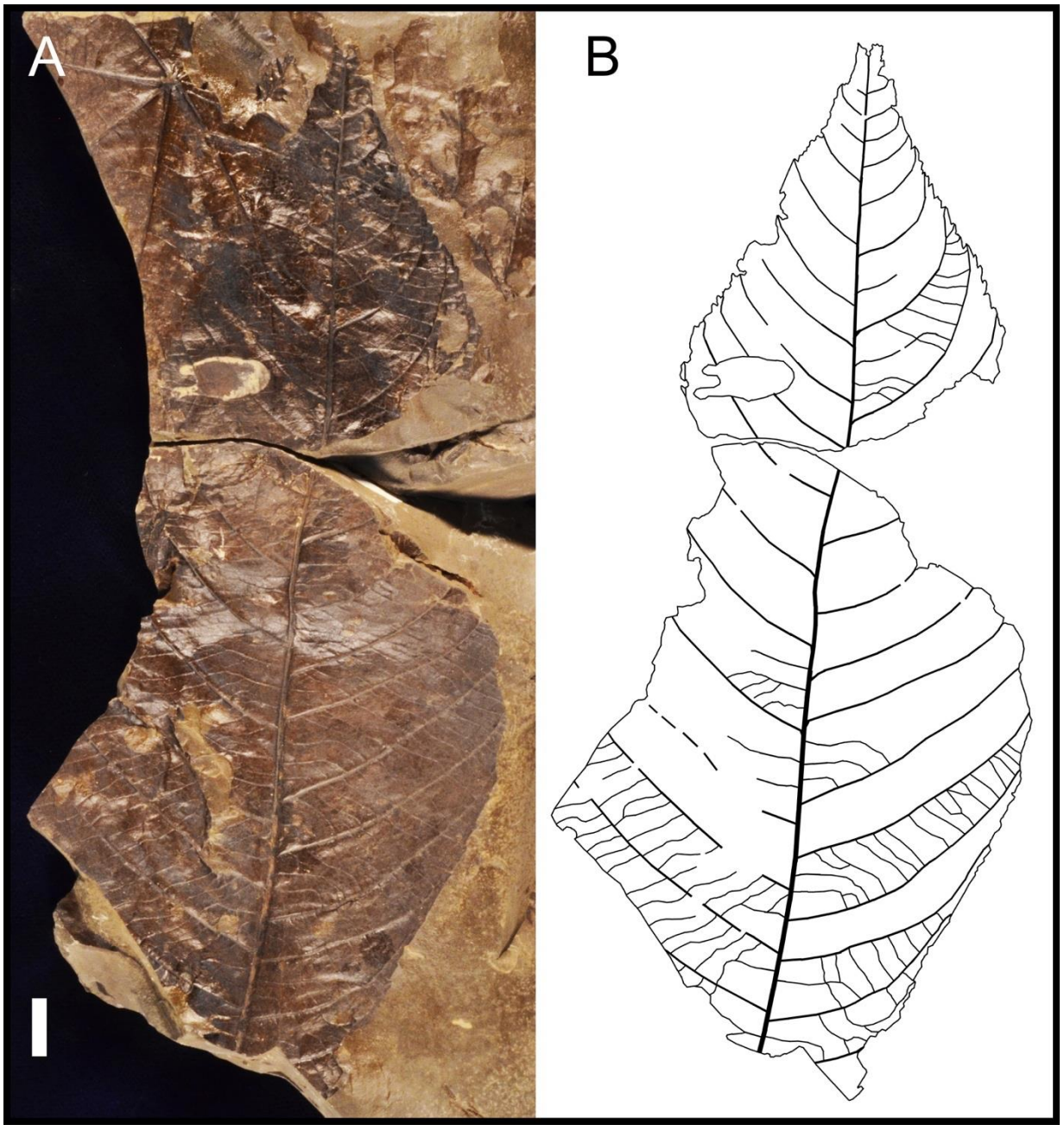

Figure 3.24: Morphotype exemplar of CAF-014, cf. '*Carya*' *antiquorum* NEWBERRY. A, USPC 436-2749. B, line drawing of the morphotype exemplar. Scale 1 cm.

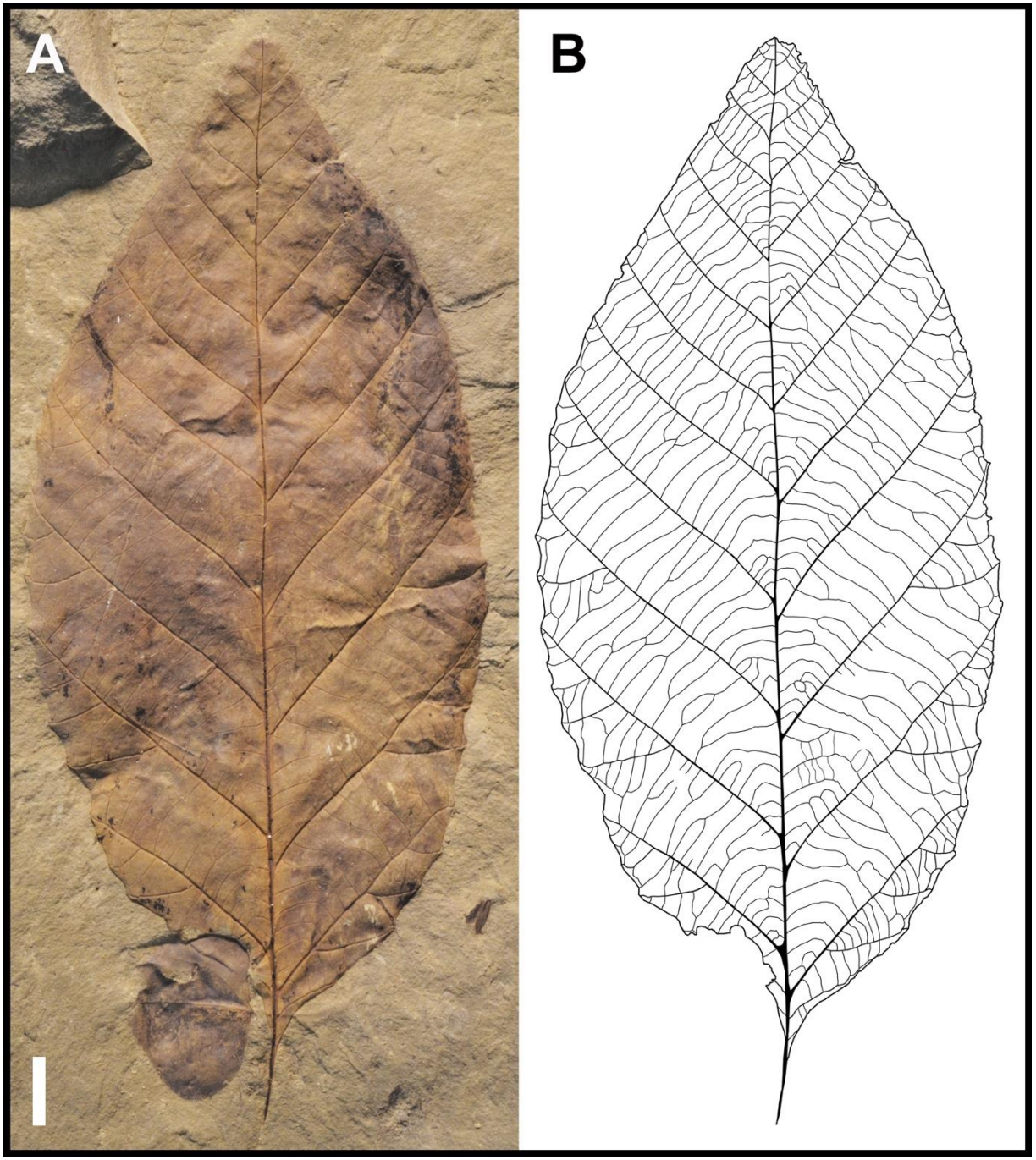

Figure 3.25: Morphotype exemplar of CAF-027, *Ushia* cf. *U. olafsenii* (HEER) BOULTER et KVAČEK. A, USPC 111-6157. B, line drawing of the morphotype exemplar. Scale 1 cm.

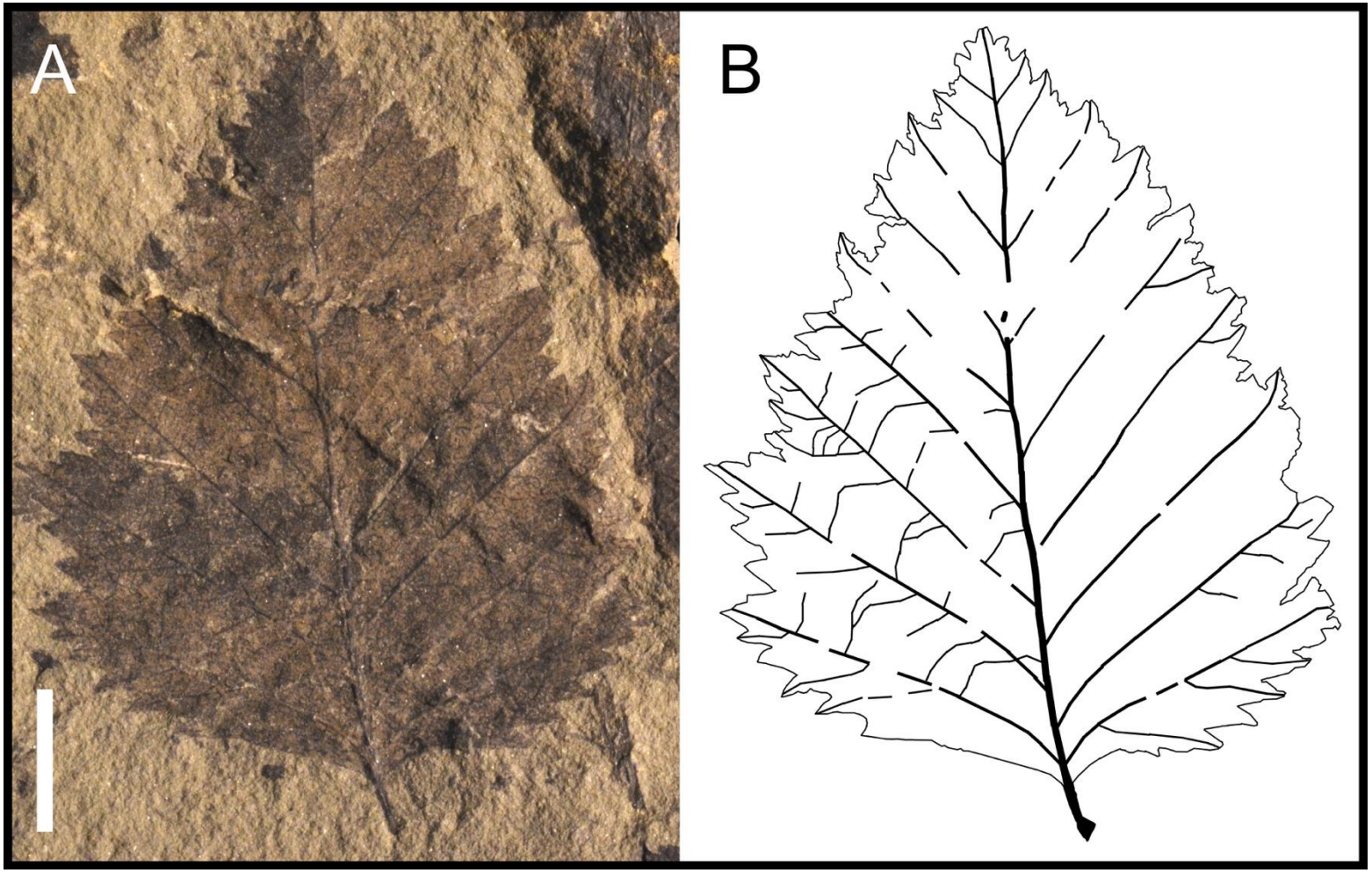

Figure 3.26: Morphotype exemplar of CAF-101, cf. *Crataegus* sp. 1. A, USPC 753-2075. B, line drawing of the morphotype exemplar. Scale 1 cm.

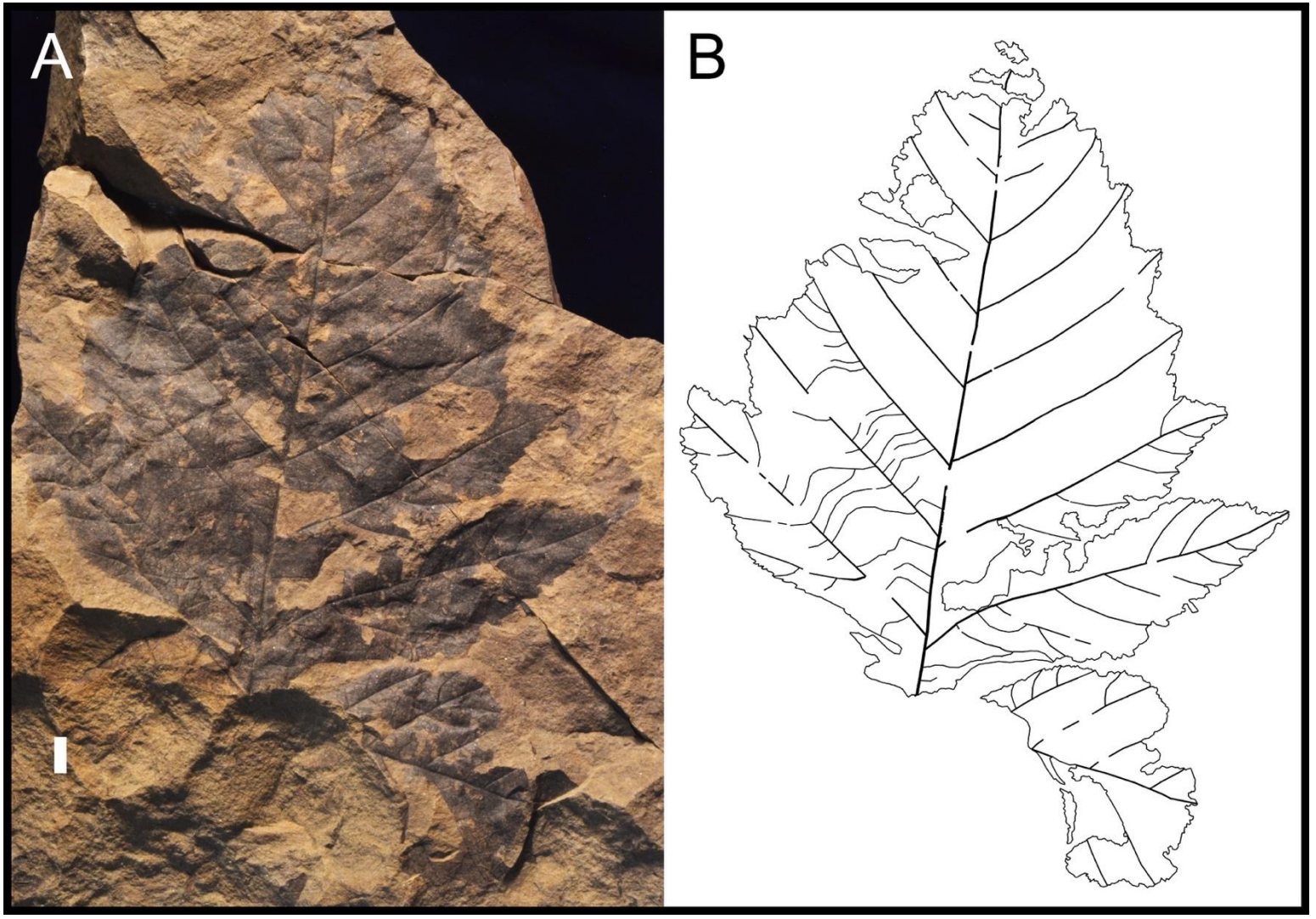

Figure 3.27: Morphotype exemplar of CAF-127, cf. *Crataegus* sp. 2. A, USPC 367-3899. B, line drawing of the morphotype exemplar. Scale 1 cm.

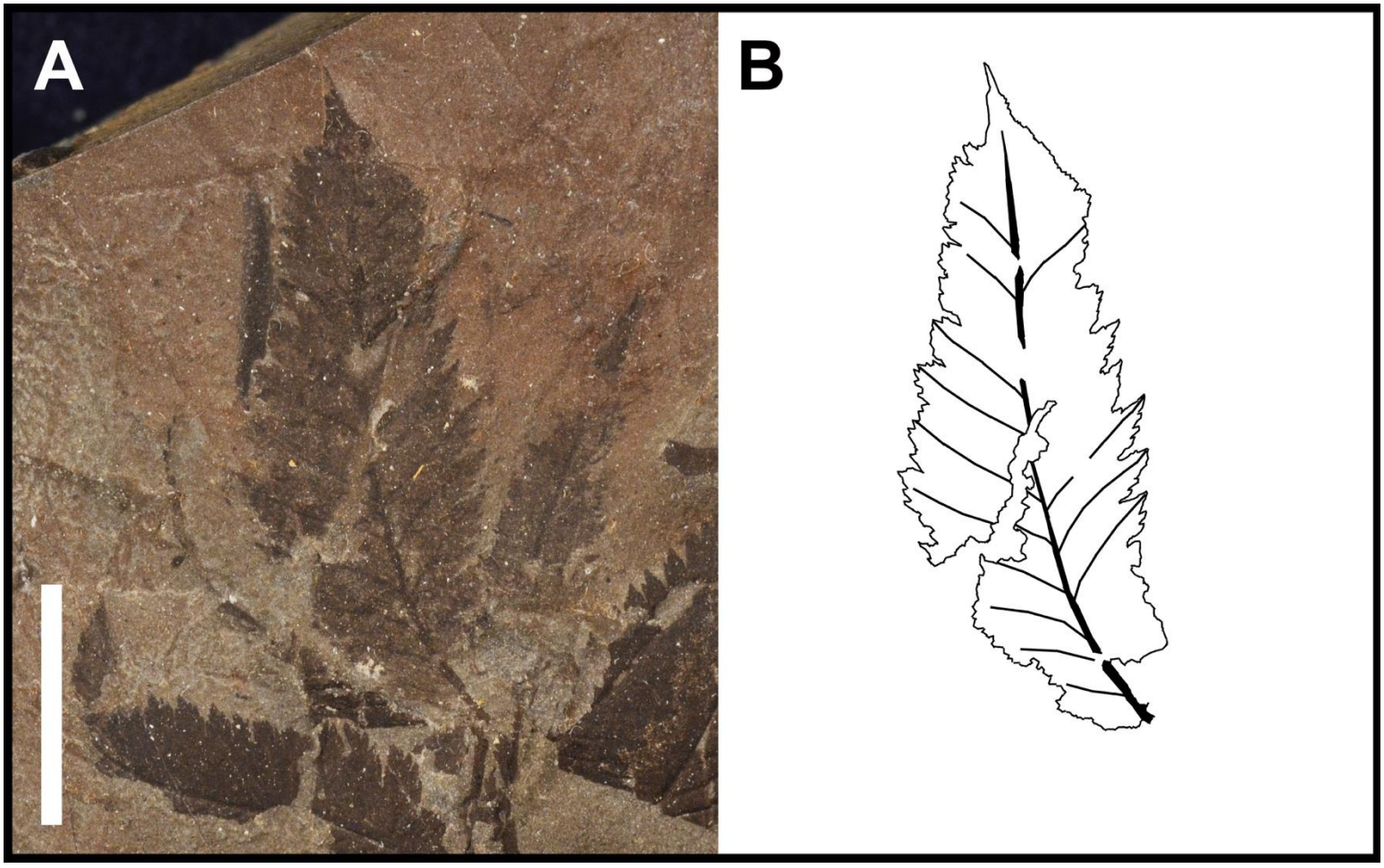

Figure 3.28: Morphotype exemplar of CAF-079, cf. *Sorbaria* aff. *S. wahrhaftigii* WOLFE et WEHR. A, YPM PB 169817. B, line drawing of the morphotype exemplar. Scale 1 cm.

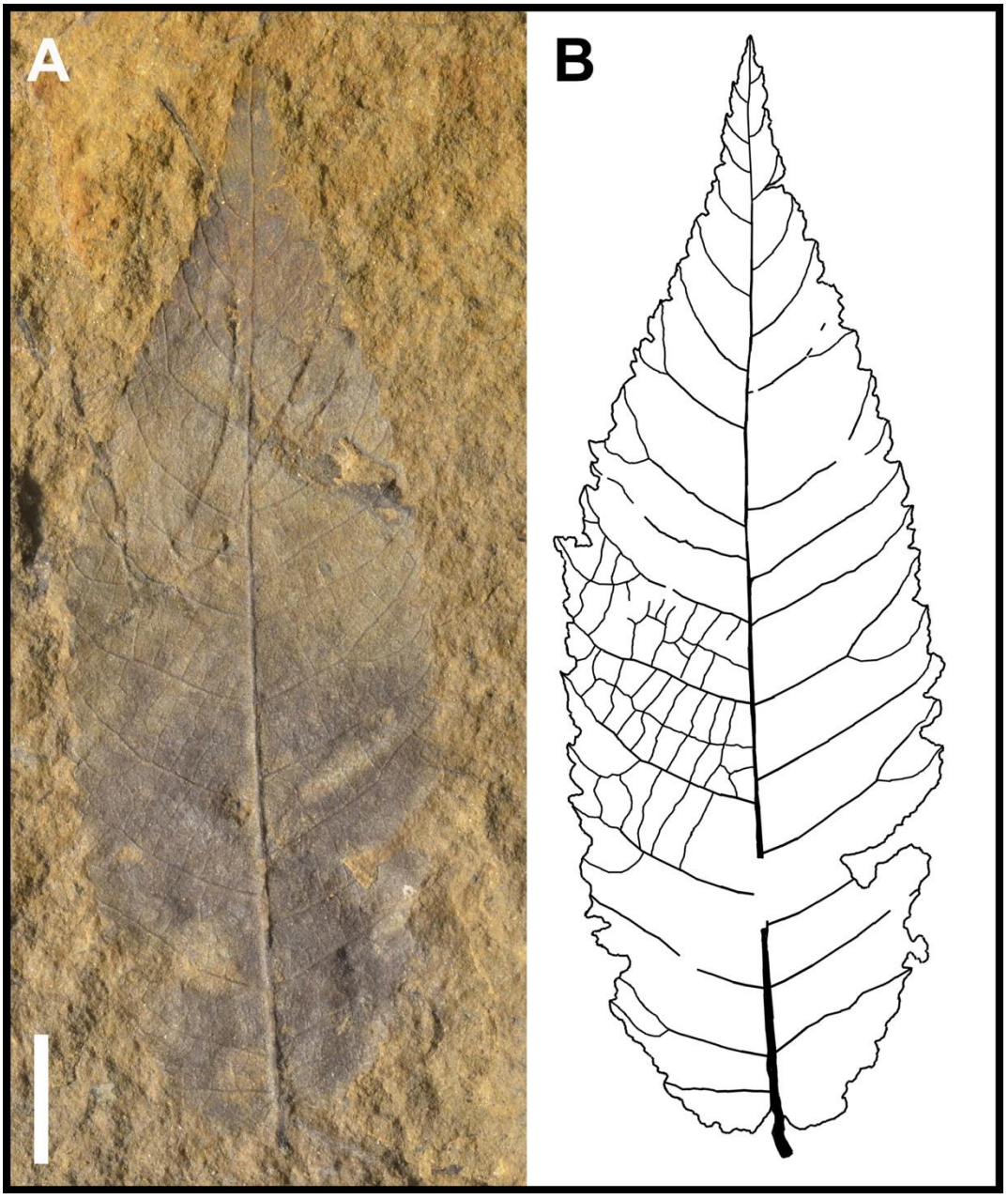

Figure 3.29: Morphotype exemplar of CAF-012, *Ulmus ulmifolia* (SCHLOEMER-JÄGER) BUDANTSEV. A, USPC 200-4809. B, line drawing of the morphotype exemplar. Scale 1 cm.

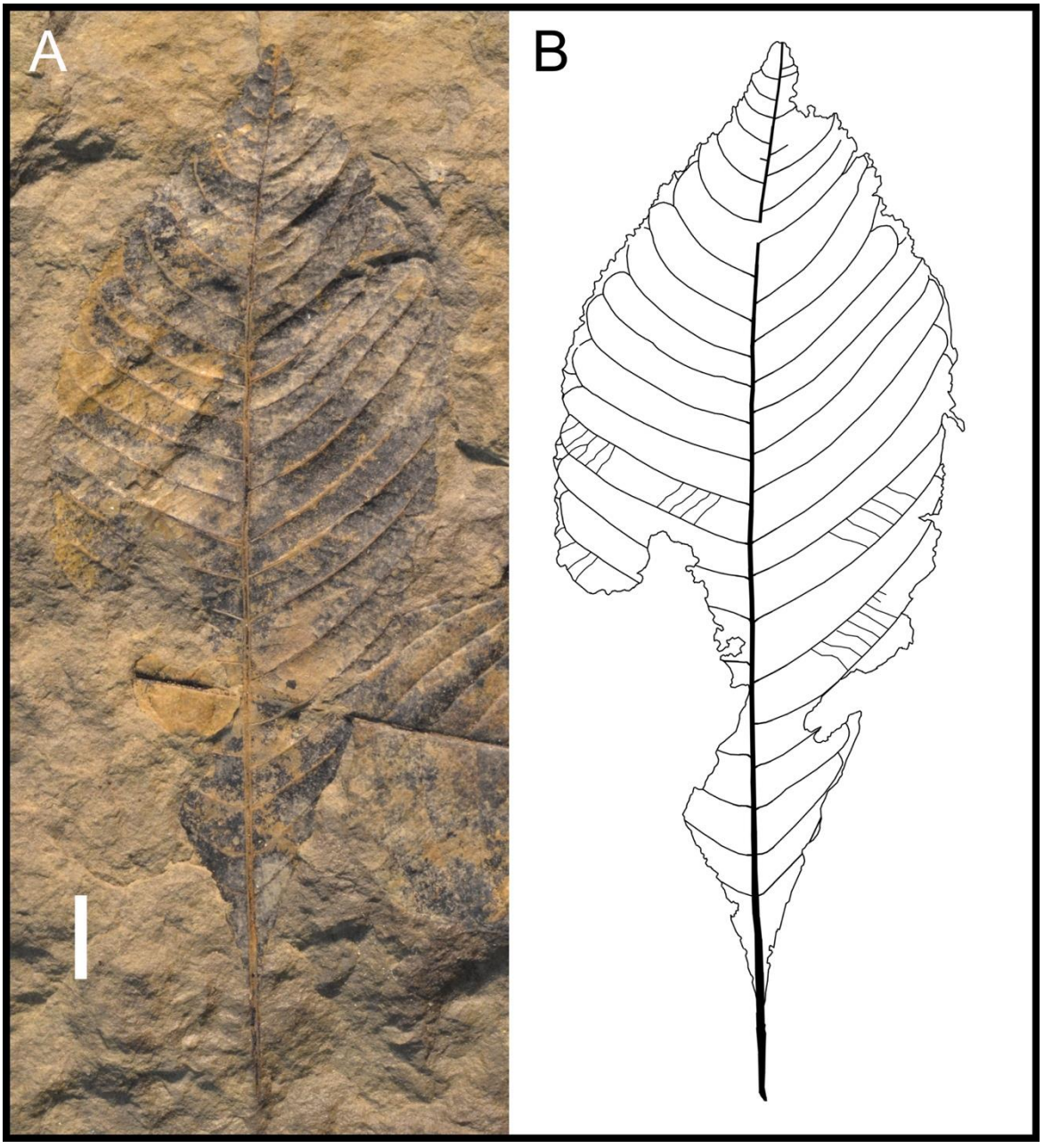

Figure 3.30: Morphotype exemplar of CAF-038, *Aesculus longipedunculus* SCHLOEMER-JÄGER. A, USPC 111-4892. B, line drawing of the morphotype exemplar. Scale 1 cm.

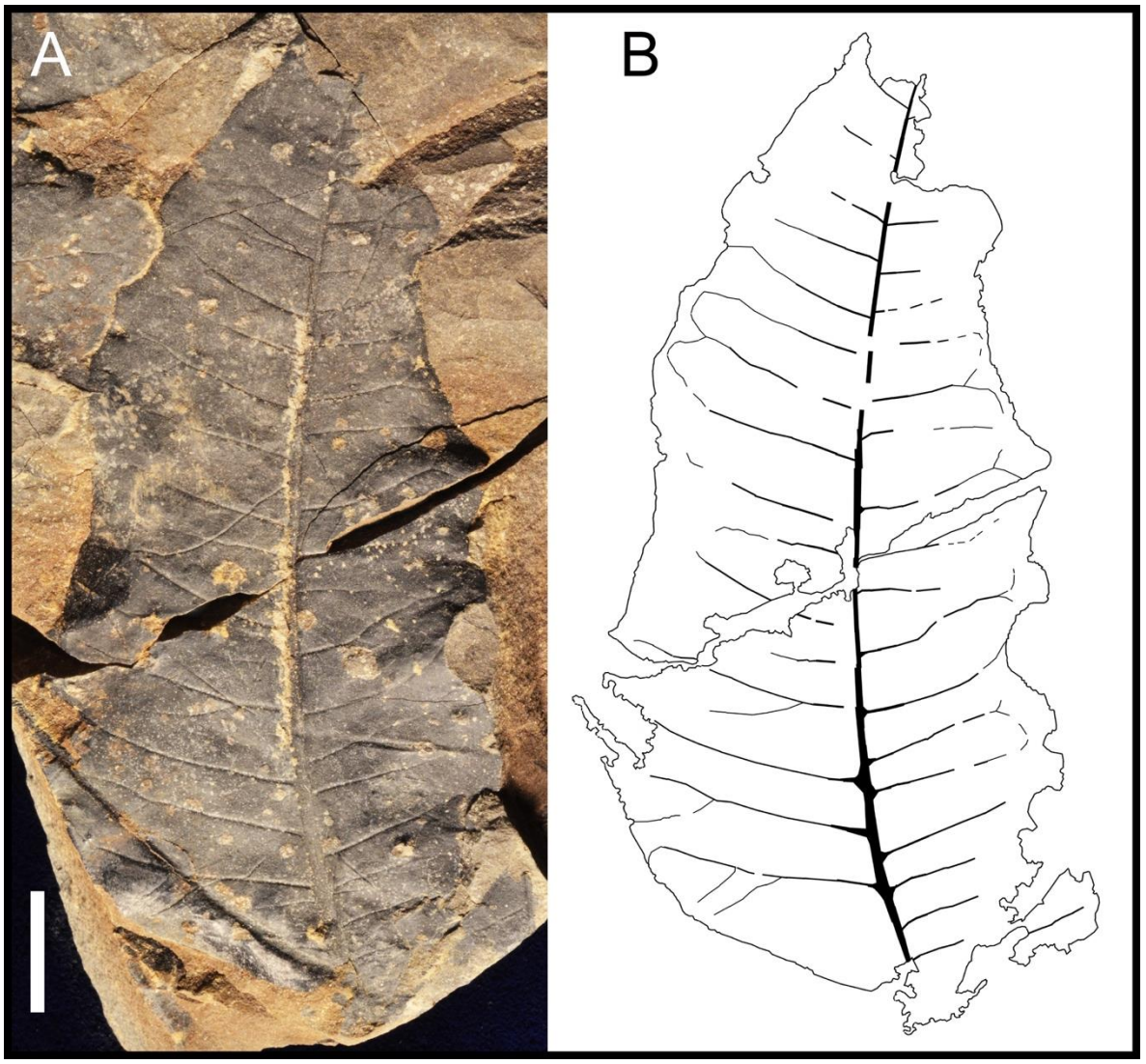

Figure 3.31: Morphotype exemplar of CAF-067, *Averrhoites* cf. *A. affinis* (NEWBERRY) HICKEY. A, USPC 178-4161. B, line drawing of the morphotype exemplar. Scale 1 cm.

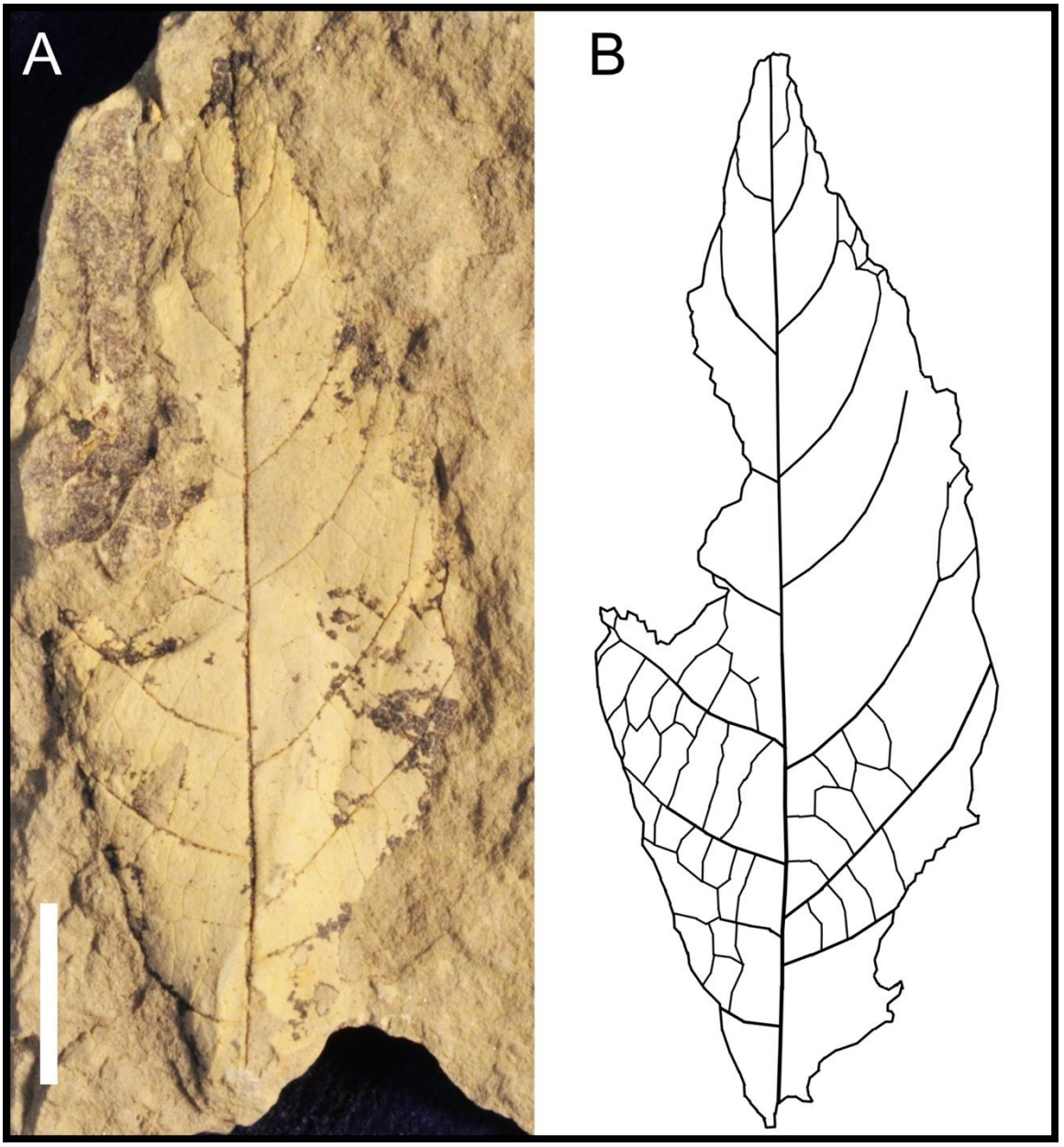

Figure 3.32: Morphotype exemplar of CAF-131, aff. *Celastrinites* sp. A, USPC 111-4917. B, line drawing of the morphotype exemplar. Scale 1 cm.

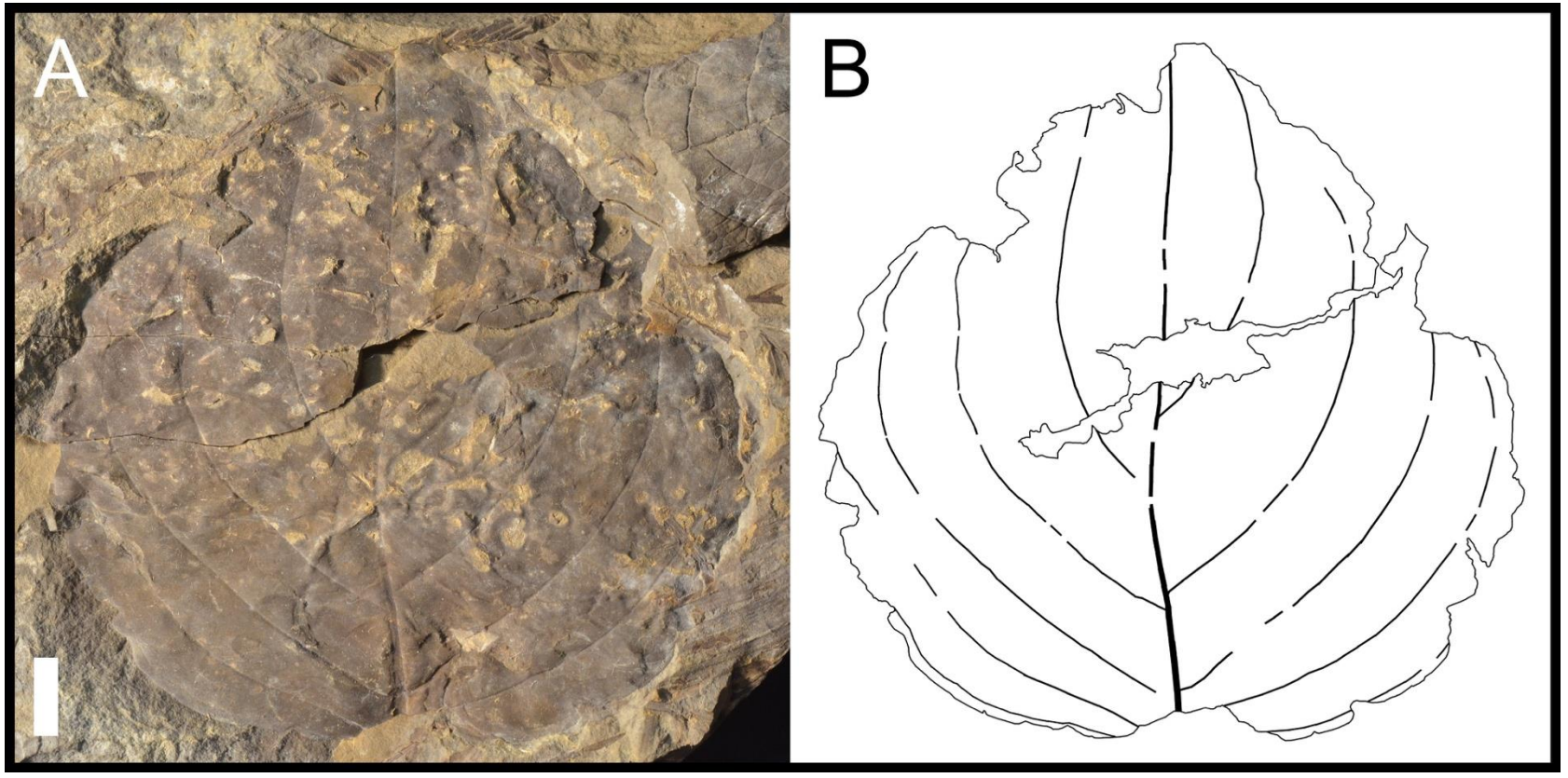

Figure 3.33: Morphotype exemplar of CAF-032, cf. *Cornophyllum* sp. Previously figured in WEST et al. 2015, figure 3 as SF021. A, USPC 438-2791. B, line drawing of the morphotype exemplar. Scale 1 cm.

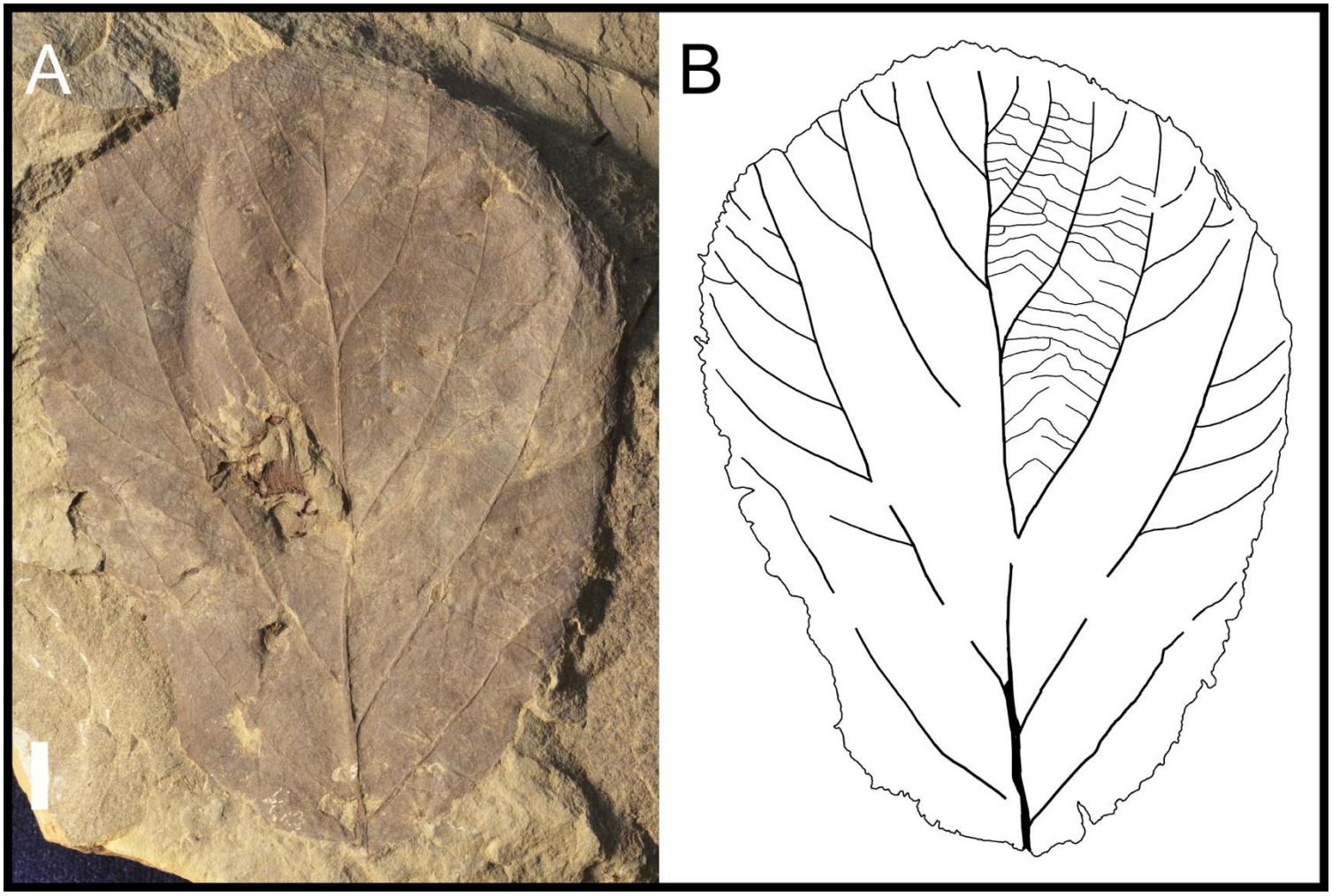

Figure 3.34: Morphotype exemplar of CAF-016. Previously figured in WEST et al. 2015, figure 3 as SF005. A, USPC 436-2769.1. B, line drawing of the morphotype exemplar. Scale 1 cm.

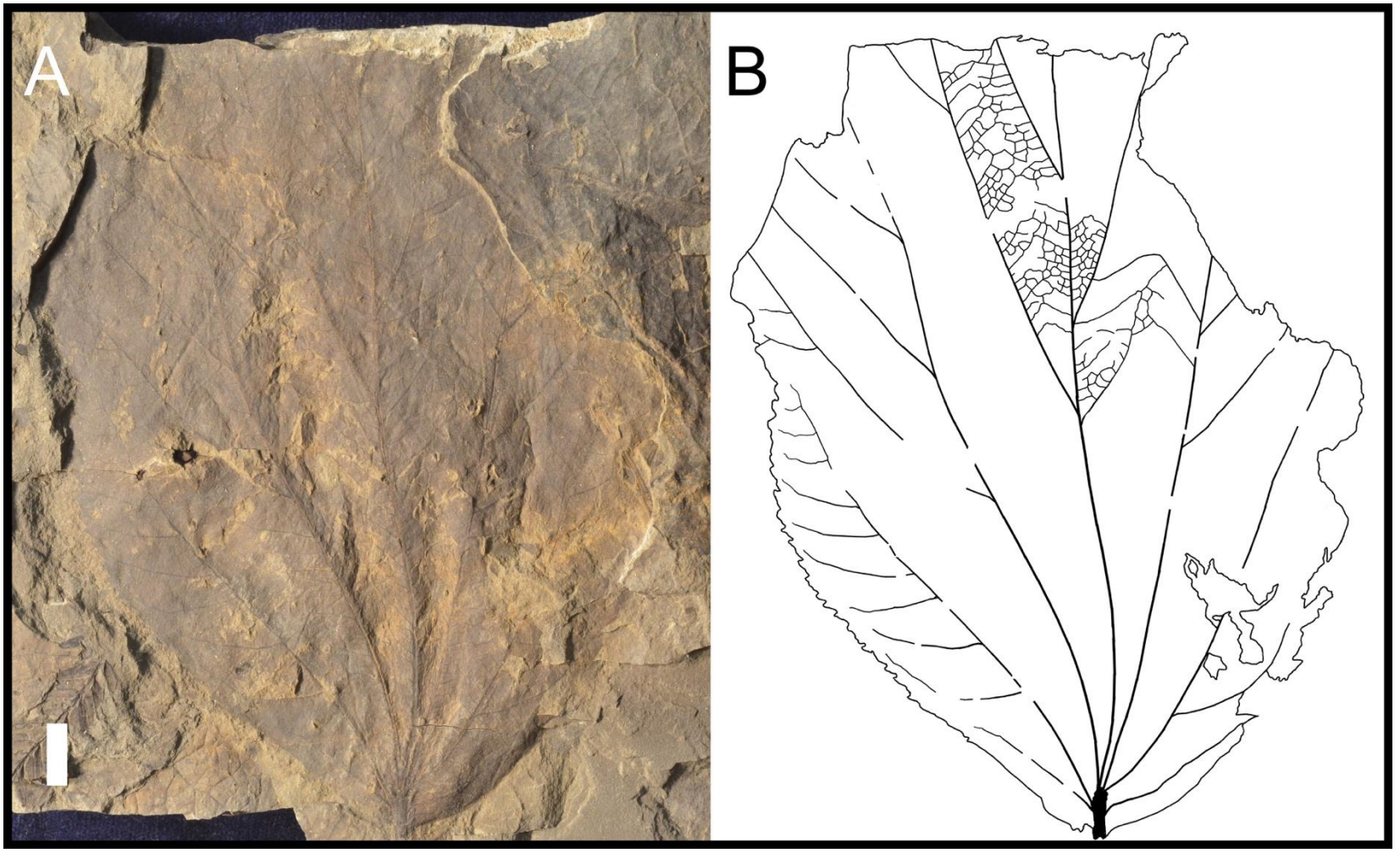

Figure 3.35: Morphotype exemplar of CAF-024. Previously figured in WEST et al. 2015, figure 3 as SF013. A, USPC 436-2752.1. B, line drawing of the morphotype exemplar. Scale 1 cm.

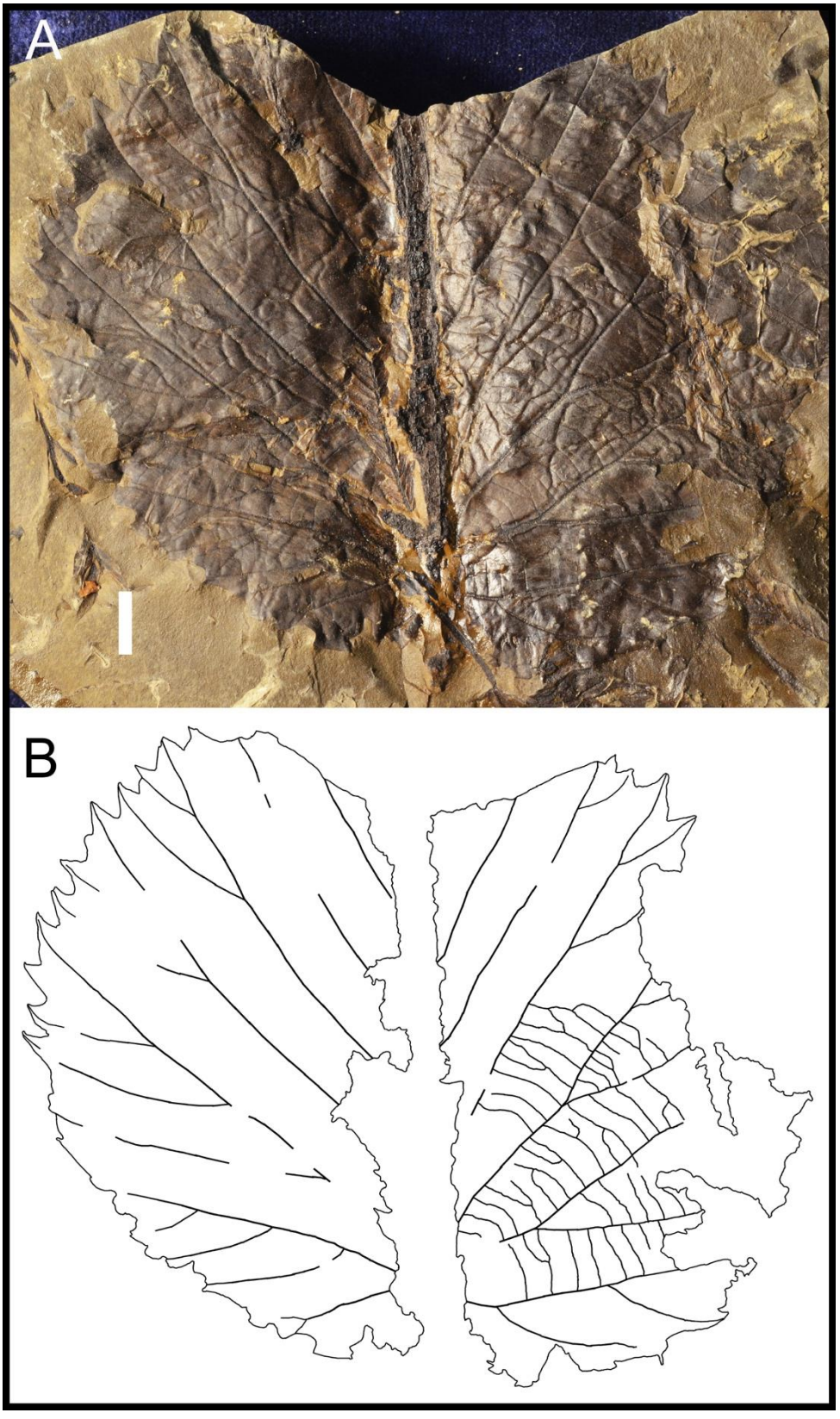

Figure 3.36: Morphotype exemplar of CAF-025. Previously figured in WEST et al. 2015, figure 3 as SF014. A, USPC 439-2801. B, line drawing of the morphotype exemplar. Scale 1 cm.

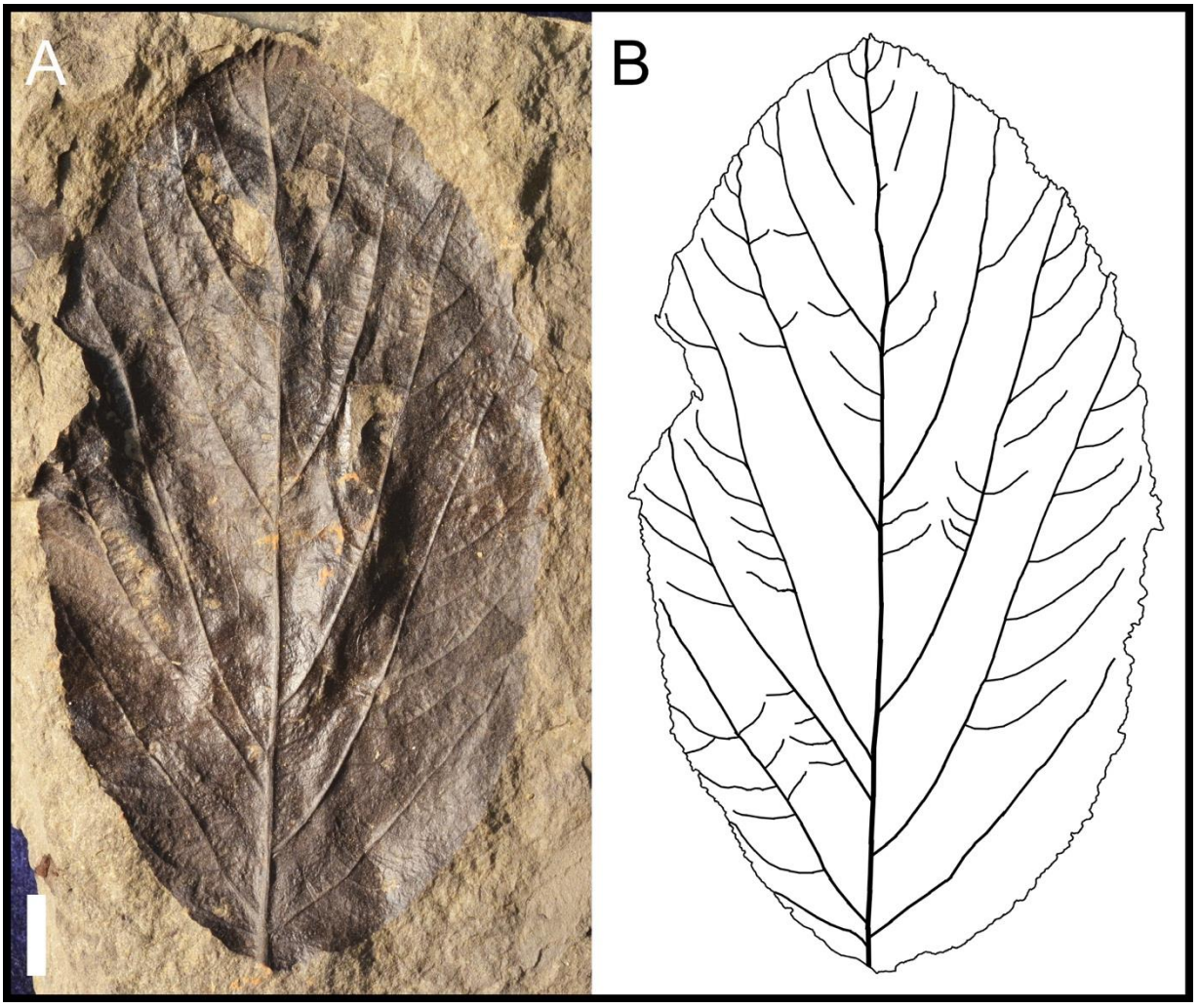

Figure 3.37: Morphotype exemplar of CAF-033. Previously figured in WEST et al. 2015, figure 3 as SF022. A, USPC 436-2735.1. B, line drawing of the morphotype exemplar. Scale 1 cm.

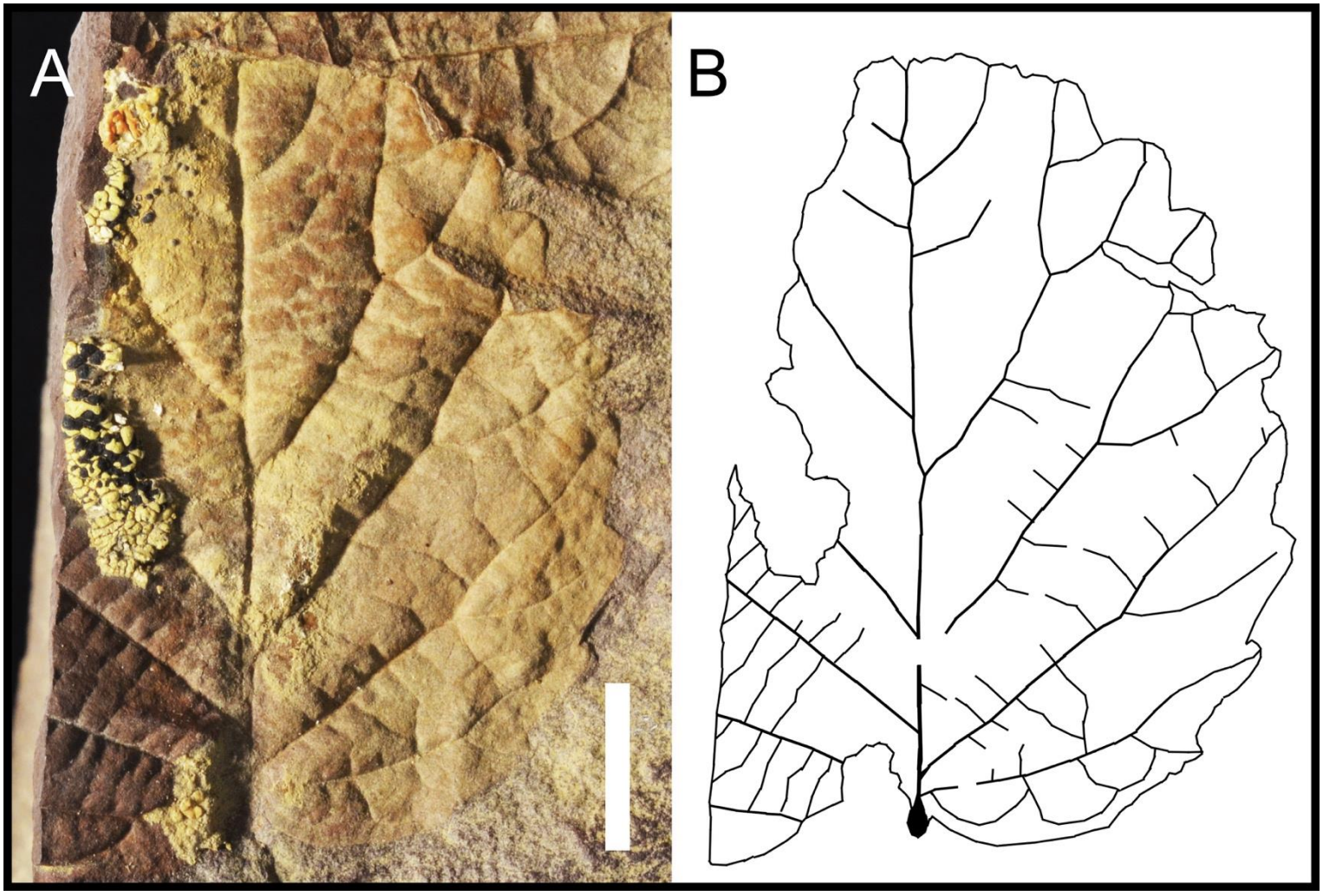

Figure 3.38: Morphotype exemplar of CAF-063. A, YPM PB 169831. B, line drawing of the morphotype exemplar. Scale 1 cm.

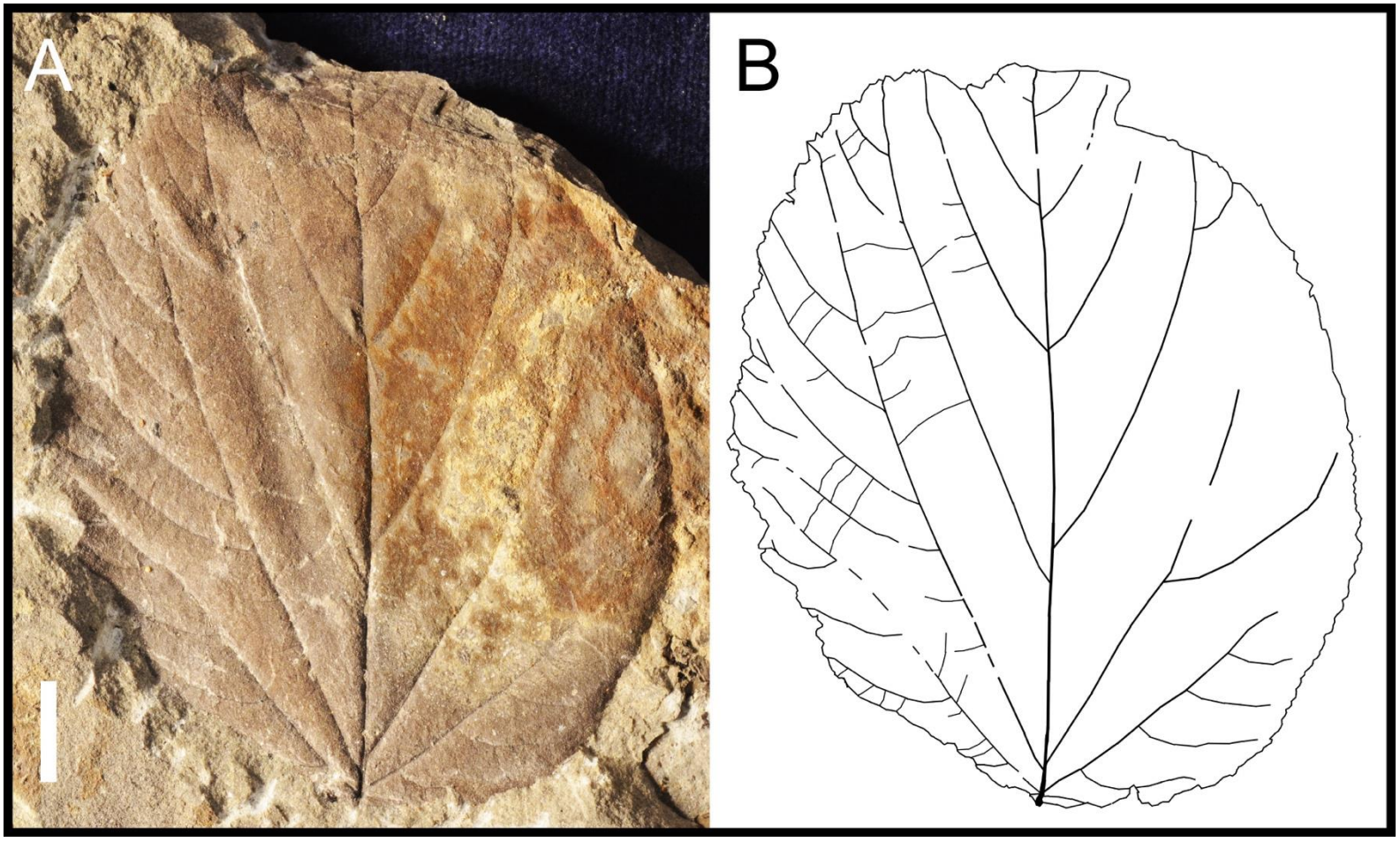

Figure 3.39: Morphotype exemplar of CAF-070. A, YPM PB 169855. B, line drawing of the morphotype exemplar. Scale 1 cm.

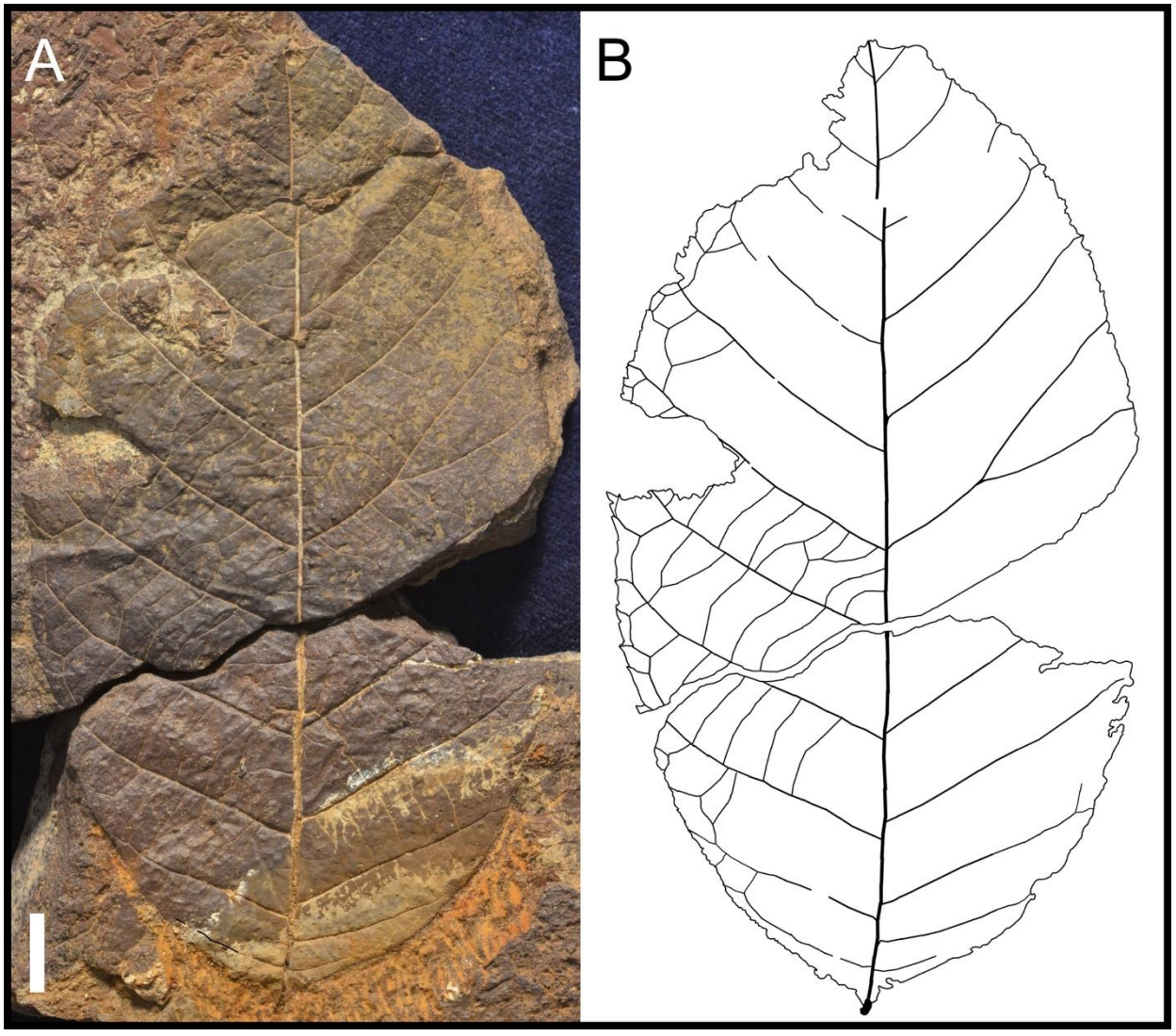

Figure 3.40: Morphotype exemplar of CAF-073. A, YPM PB 169867. B, line drawing of the morphotype exemplar. Scale 1 cm.

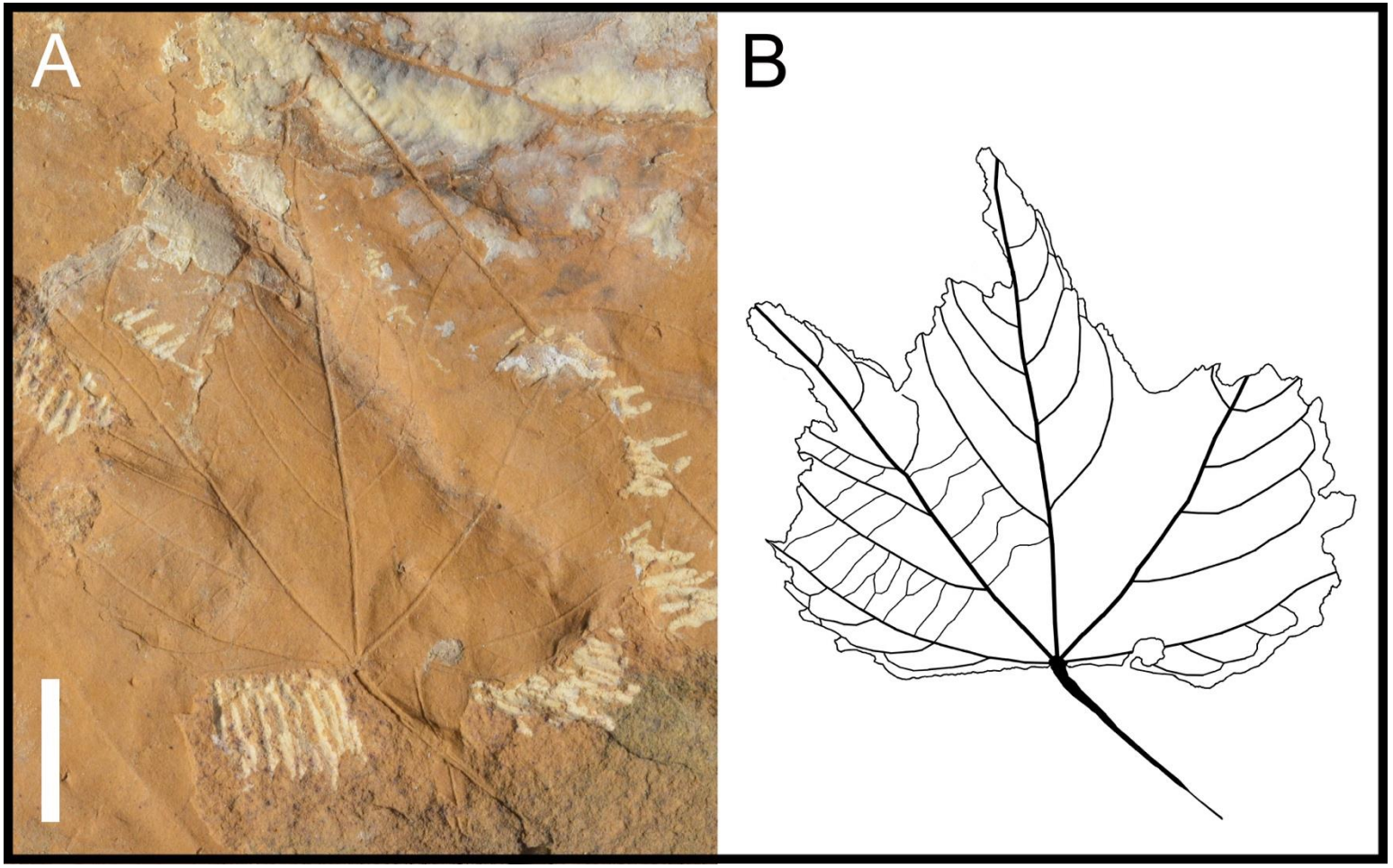

Figure 3.41: Morphotype exemplar of CAF-076. A, YPM PB 169805. B, line drawing of the morphotype exemplar. Scale 1 cm.

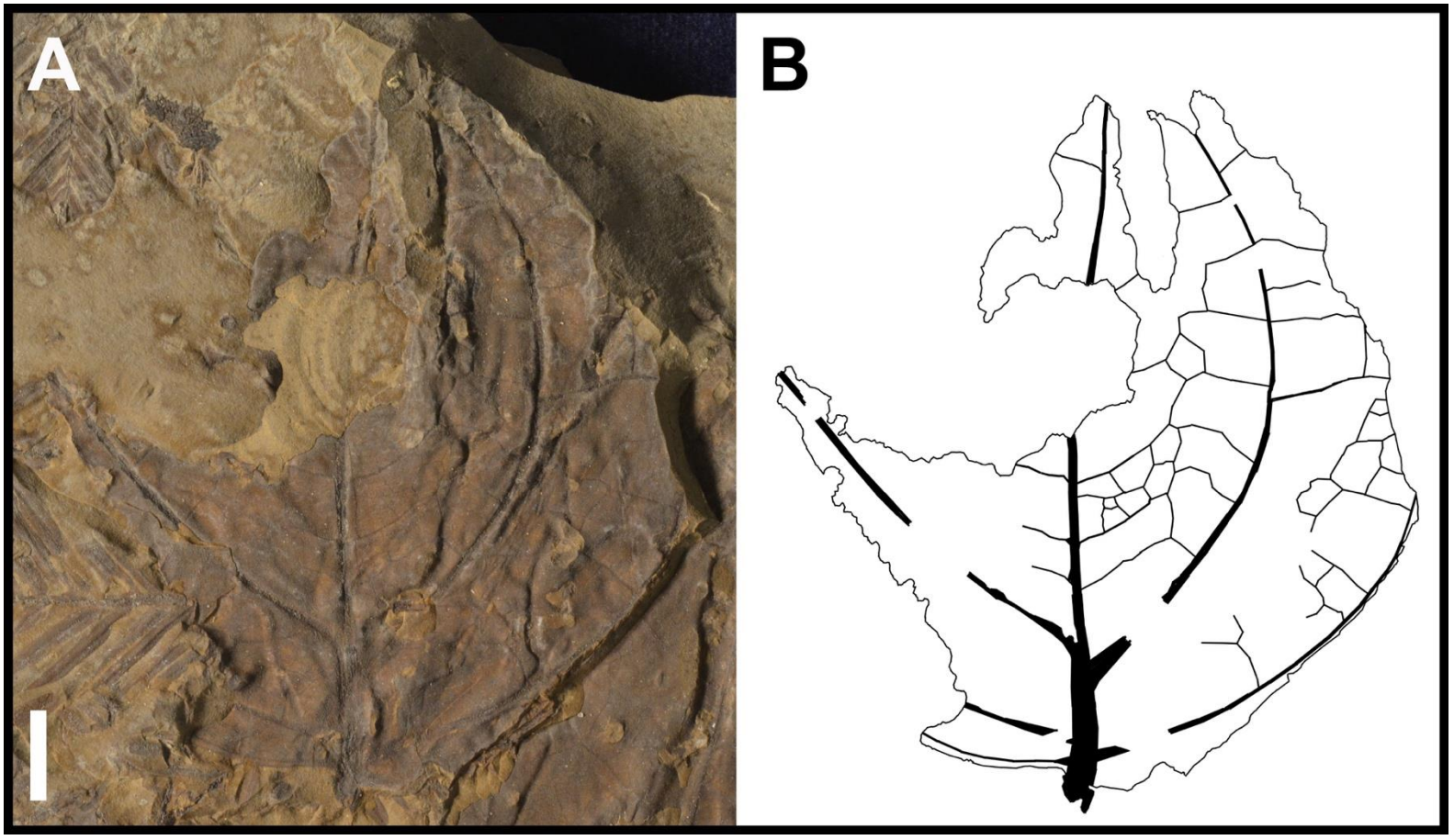

Figure 3.42: Morphotype exemplar of CAF-100. A, YPM PB 169928. B, Line drawing of the morphotype exemplar. Scale 1 cm.

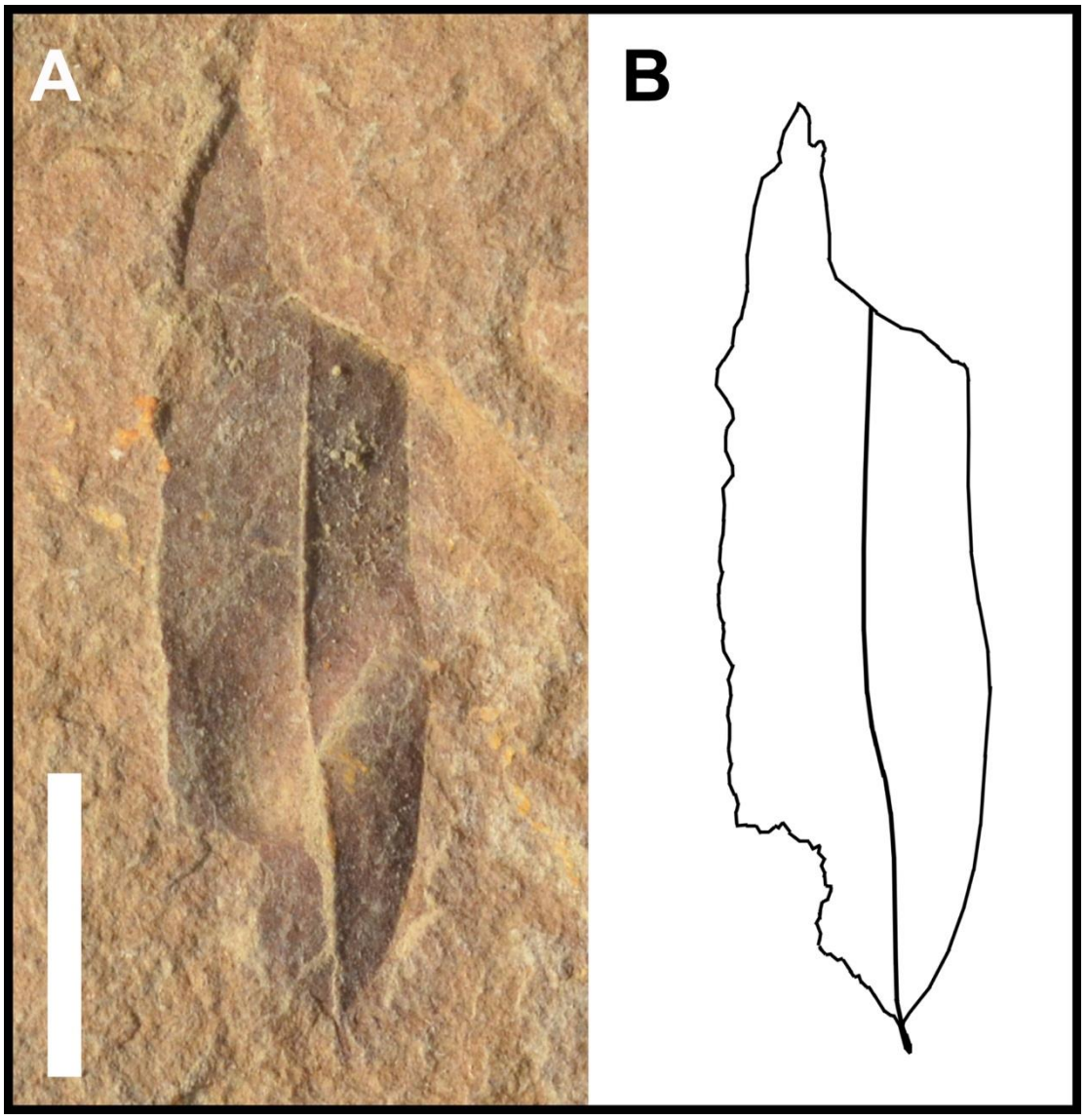

Figure 3.43: Morphotype exemplar of CAF-103. A, YPM PB 169925. B, line drawing of the morphotype exemplar. Scale 1 cm.

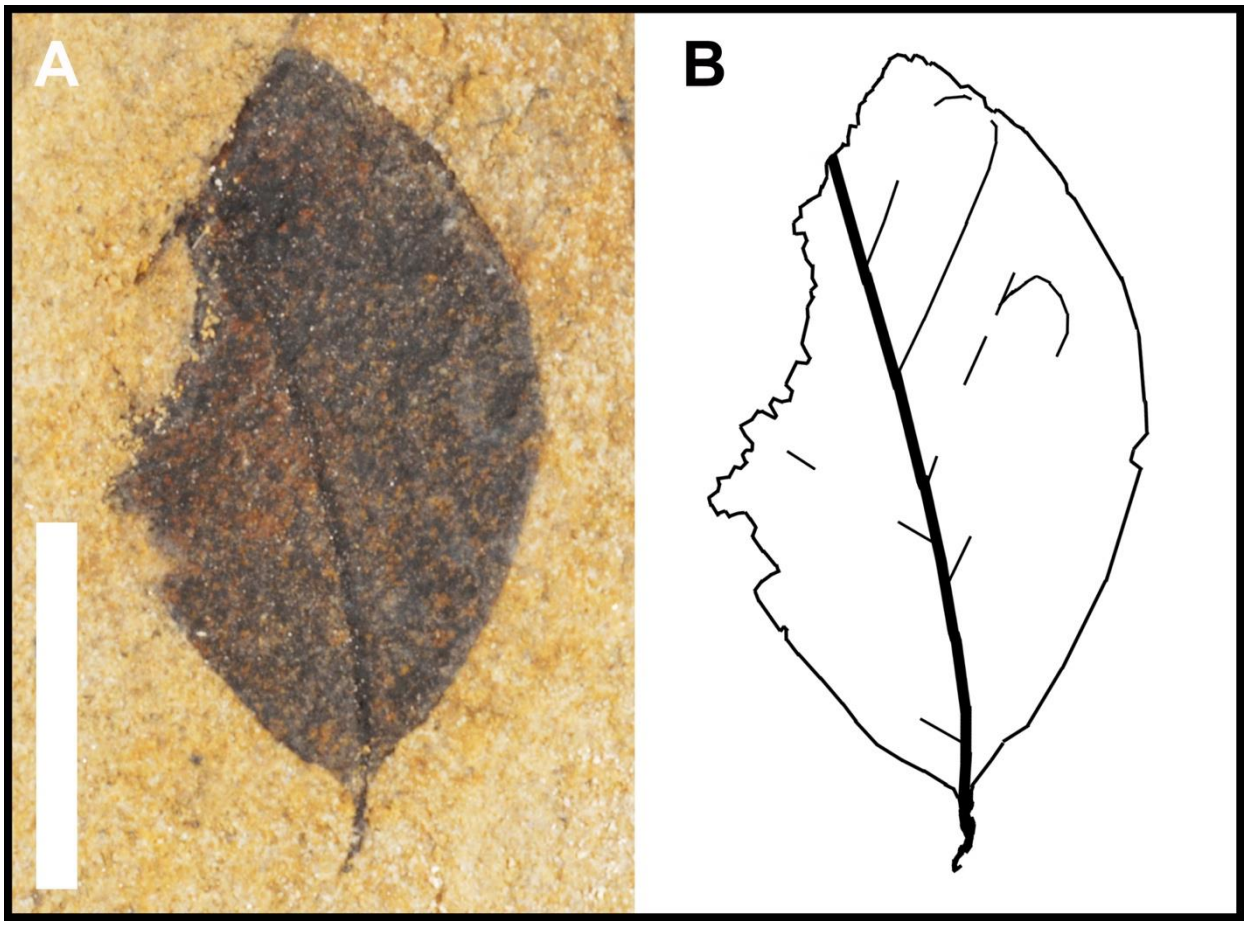

Figure 3.44: Morphotype exemplar of CAF-104. A, USPC 175-4113. B, line drawing of the morphotype exemplar. Scale 1 cm.

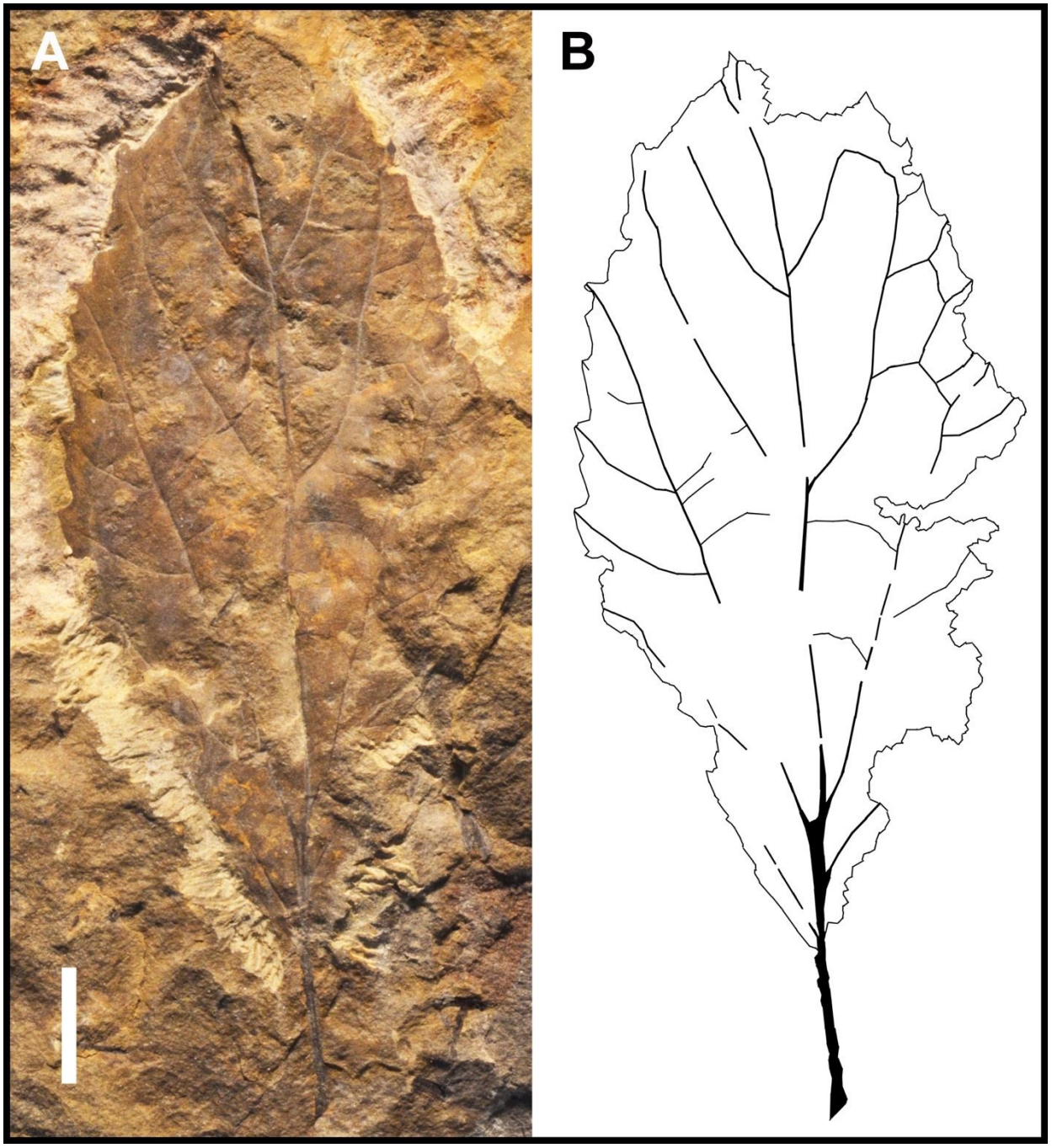

Figure 3.45: Morphotype exemplar of CAF-130. A, USPC 200-4771. B, line drawing of the morphotype exemplar. Scale 1 cm.

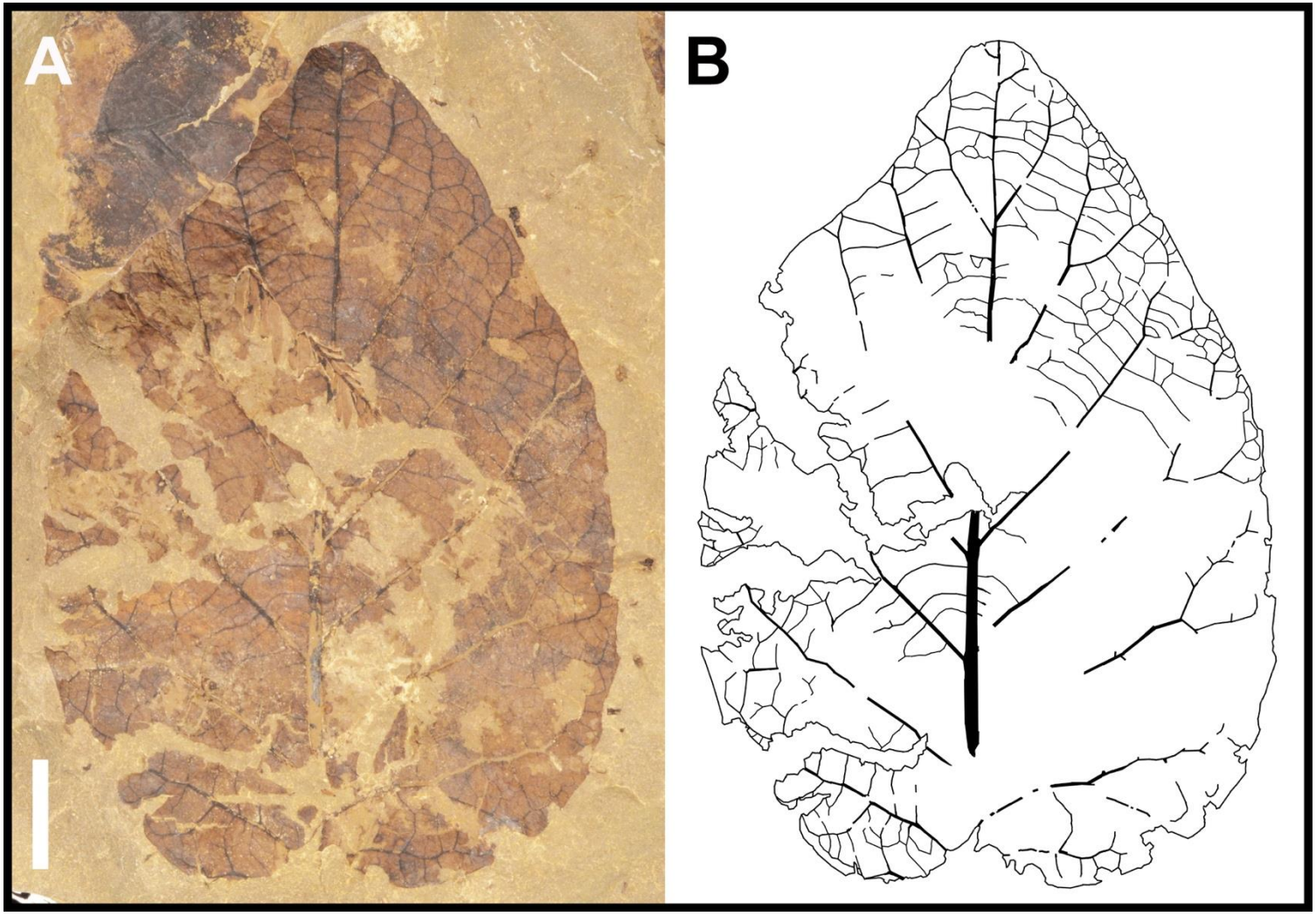

Figure 3.46: Morphotype exemplar of CAF-132. A, USPC 111-4933. B, line drawing of the morphotype exemplar. Scale 1 cm.

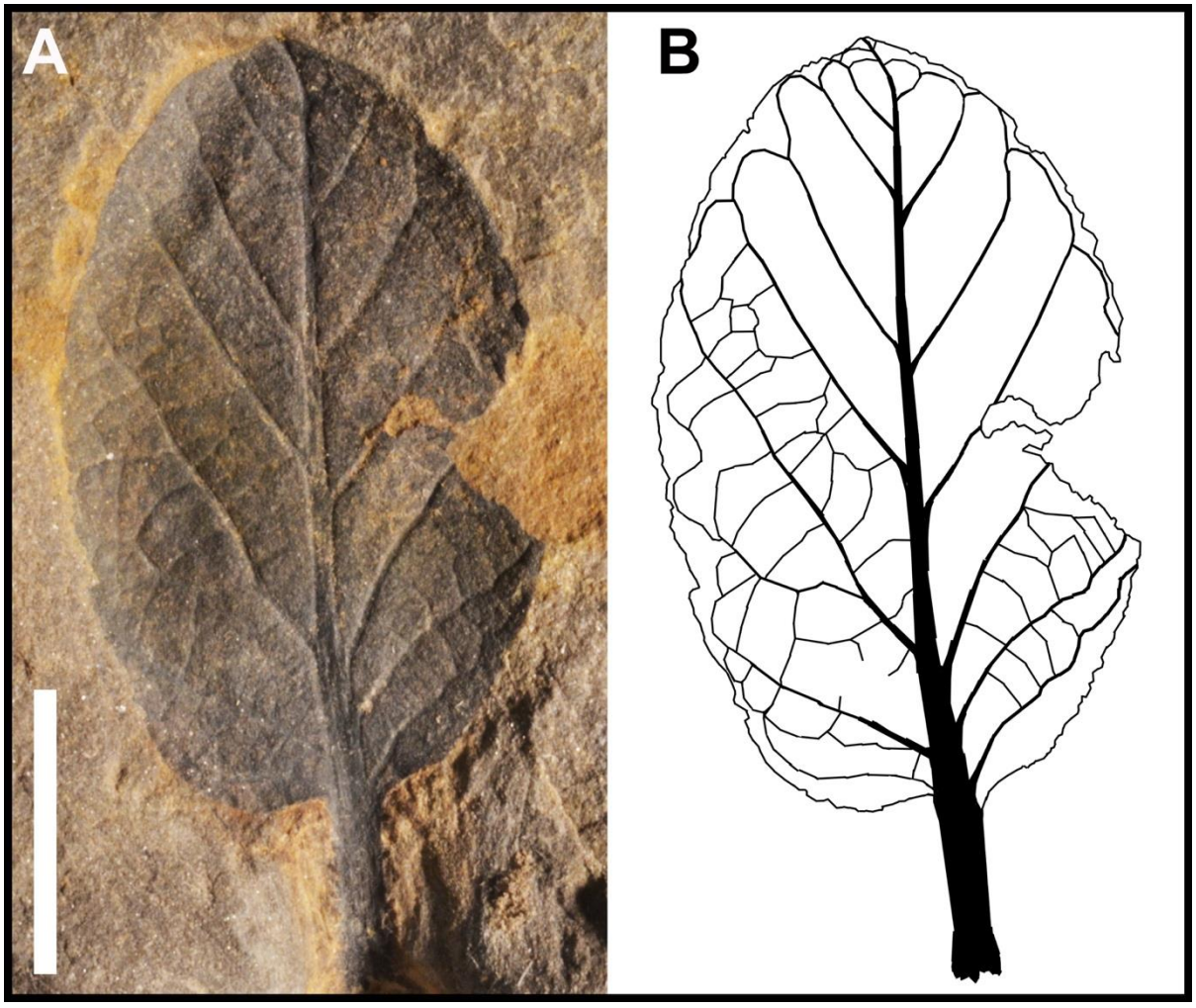

Figure 3.47: Morphotype exemplar of CAF-151. A, USPC 171-4260. B, line drawing of the morphotype exemplar. Scale 1 cm.

Plate I

Fig. 1-9. *Equisetum* sp.

1. Morphotype exemplar of stems, scale 1 cm, USPC 715-2230
2. Leaf collar showing narrow teeth with acute apices, scale 1 cm, USPC 442-2819
3. Branch with internode, scale 1 cm, USPC 22-1175
4. Rhizome, scale 1 cm, USPC 111-4927
5. Rhizome with probable spherical tubers, scale 1 cm, USPC 753-2138
6. Rhizome with adventitious roots at nodes, scale 1 cm, USPC 712-2222
7. Rhizome cross-section showing whorled tubers and possible rootlets, scale 1 cm, USPC 361-3919
8. Branch with internode, scale 1 cm, USPC 715-2228
9. Cross-section of nodal diaphragm with large pith cavity of axis, scale 1 cm, USPC 715-2228

Fig. 10. *Osmunda macrophylla* PENHALLOW, frond of morphotype exemplar, scale 1 cm, USPC 105-4717

Fig. 11. *Azolla* sp., branching rhizome of morphotype exemplar showing leaves and roots, scale 1 cm, USPC 370-3823

Fig. 12. *Salvinia* cf. *S. preauriculata* BERRY, morphotype exemplar, leaf fragment, scale 1 cm, YPM PB 169878

Fig. 13. *Coniopteris blomstrandii* (HEER) KVAČEK et MANUM, morphotype exemplar, sterile pinnae, scale 1 cm, USPC 759-2202

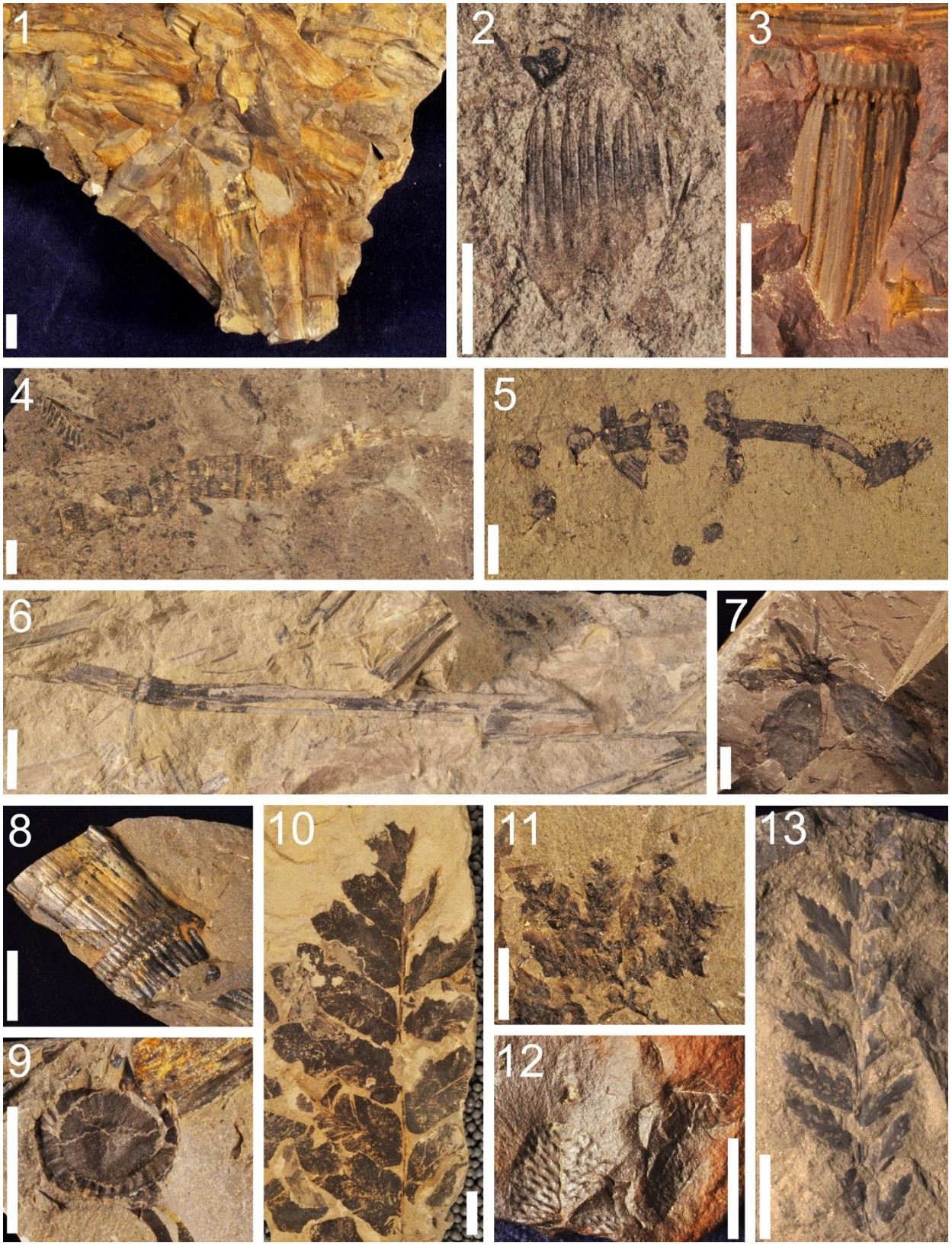
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Plate II

Fig. 1-2. *Coniopteris blomstrandii* (HEER) KVAČEK et MANUM

1. Sterile pinnae showing well preserved pinnules with acute apices and crenate margin, scale 1 cm, USPC 175-4115
2. Sterile pinnae showing pinnules with open dichotomous venation, scale 1 cm, USPC 22-1229

Fig. 3. aff. Pinaceae, Gen indet. sp. indet. Morphotype CAF-115, morphotype exemplar, seed cone, scale 1 cm, YPM PB 169921

Fig. 4. *Cunninghamia* sp., morphotype exemplar, scale 1 cm, YPM PB 169858

Fig. 5-8 *Metasequoia occidentalis* (NEWBERRY) CHANEY

5. Pollen cones, scale 1 cm, USPC 439-2804
6. Seed cone, scale 1 cm, USPC 200-4765
7. Foliar morphotype exemplar, scale 1 cm, USPC 178-4156
8. 2-winged seeds, scale 1 cm, USPC 251-3602

Fig. 9-13. *Glyptostrobus nordenskioldii* (HEER) BROWN

9. Foliar morphotype exemplar showing leaf polymorphism, scale 1 cm, USPC 111-4954
10. Branch with leaves and attached seed cone, scale 1 cm, USPC 250-3670
11. Seed cone, scale 1 cm, USPC 255-3791
12. Pollen cones, scale 1 cm, USPC 111-4951
13. Pollen cones, scale 1 cm, USPC 111-4951

Fig. 14. *Elatocladus cordillera* CHRISTOPHEL, morphotype exemplar, scale 1 cm, USPC 436-2742

Fig 15. *Ginkgo adiantoides* (UNGER) HEER, morphotype exemplar, scale 1 cm, USPC 111-4886


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Plate III

Fig. 1-2. *Thuja polaris* MCIVER et BASINGER

1. Scale 1 cm, USPC 101-3393, previously figured as Fig. 2 in MCIVER & BASINGER 1989a
2. Morphotype exemplar, scale 1 cm, USPC 101-3393, previously figured as Fig. 3 in MCIVER & BASINGER 1989a

Fig. 3. gen. indet. sp. indet. Morphotype CAF-085, morphotype exemplar showing strong parallel straight venation, scale 1 cm, YPM PB 169824

Fig. 4. gen. indent. sp. indet. Morphotype CAF-148, morphotype exemplar with robustly keeled leaves, scale 1 cm, USPC 261-6326

Fig. 5 & 12. *Cupressinocladus* sp. 1

5. Foliar morphotype exemplar showing alternate branching, scale 1 cm, YPM PB 169897
12. Additional foliar specimen on morphotype exemplar sample, scale 1 cm, YPM PB 169897

Fig. 6 & 8 *Cupressinocladus sp.* 2

6. Morphotype exemplar, scale 1 cm, USPC 753-2129
8. Branch showing well preserved scale-lake decussate leaves, scale 1 cm, USPC 753-2123

Fig. 7. gen. indent. sp. indet. Morphotype CAF-152, morphotype exemplar, scale 1 cm, USPC 166-4267

Fig. 9-10. gen. indent. sp. indet. Morphotype CAF-139

9. Cone scale morphotype exemplar showing chewed or toothed distal edge, scale 1 cm, USPC 23-1270
10. Cone scale showing entire distal margin, scale 1 cm, USPC 23-1266

Fig. 11. cf. *Magnolia* sp., specimens showing entire margin and brochidodromous secondary venation, scale 1 cm, USPC 111-4885

Fig. 13. *Zingiberopsis* cf. *Z. isonervosa* HICKEY, morphotype exemplar showing secondary veins diverging from midrib at acute angles, scale 1 cm, USPC 100-6260

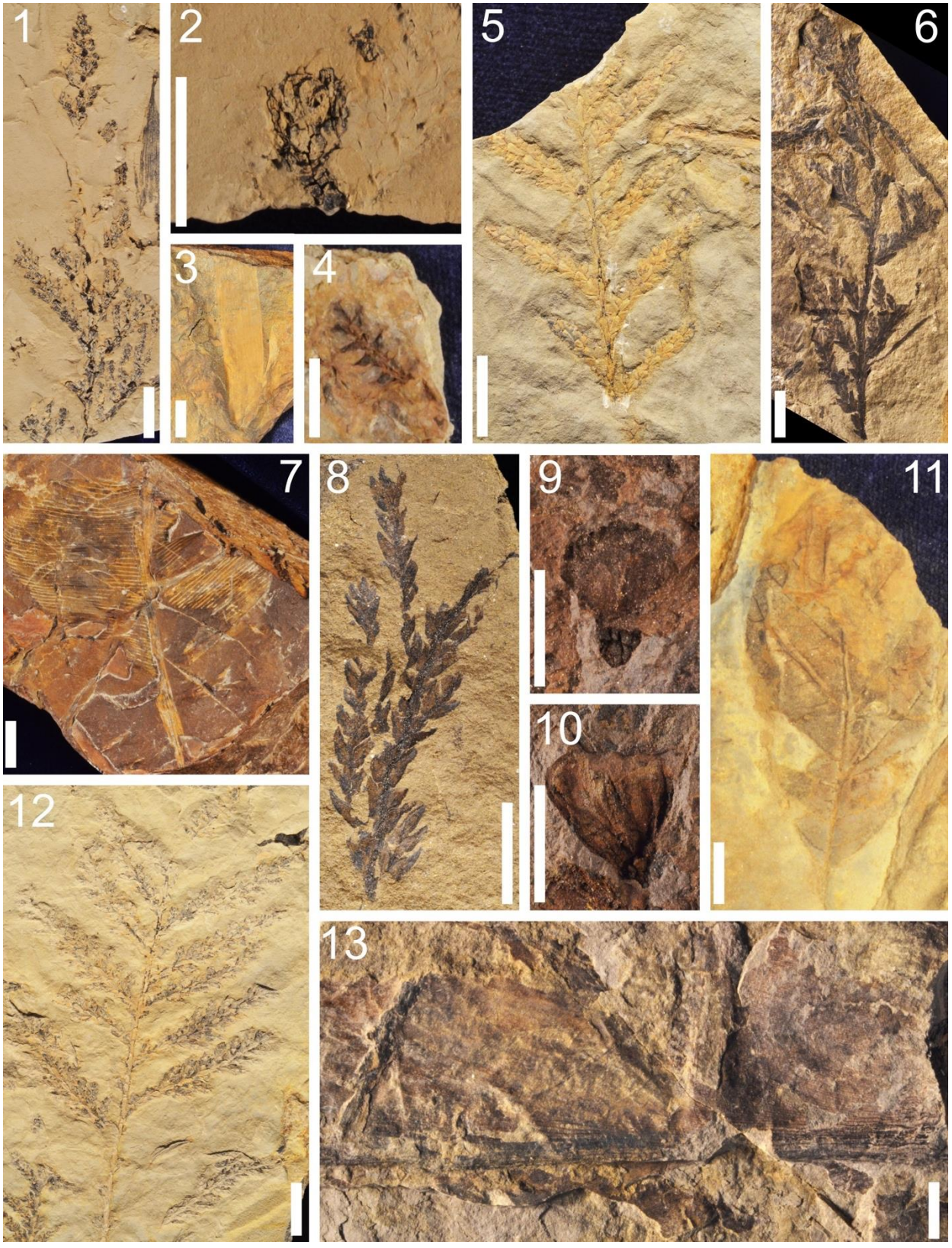
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Fig. 1 & 3 gen. indet. sp. indet. Morphotype CAF-133

1. Morphotype exemplar showing the robust costa and major secondary parallel venation, scale 1 cm, USPC 437-2782
3. Close-up of Figure 1 showing the major secondary venation departing from the costa nearly orthogonally, scale 1 cm, USPC 437-2782

Fig. 2. gen. indent. sp. indet. Morphotype CAF-096, morphotype exemplar showing primary venation sets, scale 1 cm, YPM PB 169875

Fig. 4-5. cf. *Nelumbo* sp.

4. Morphotype exemplar showing prominent straight basal veins, scale 1 cm, YPM PB 169879
5. Close-up of Figure 4 showing a prominent central disc, scale 1 cm, YPM PB 169879

Fig. 6-8. *Macginitiea* aff. *M. nobilis* (NEWBERRY) MANCHESTER

6. Leaf apex showing brochidodromous secondary venation and untoothed margin, scale 1 cm, USPC 1012-12068 (NUPB 724)
7. Foliar specimen with robust palinactinodromous primary venation, scale 1 cm, USPC 1012-12064 (NUPB 720)
8. Long *Macginitiea* petiole inserting into palinactinodromous venation, arrows for clarity, scale 1 cm, USPC 1012-12074 (NUPB 730)

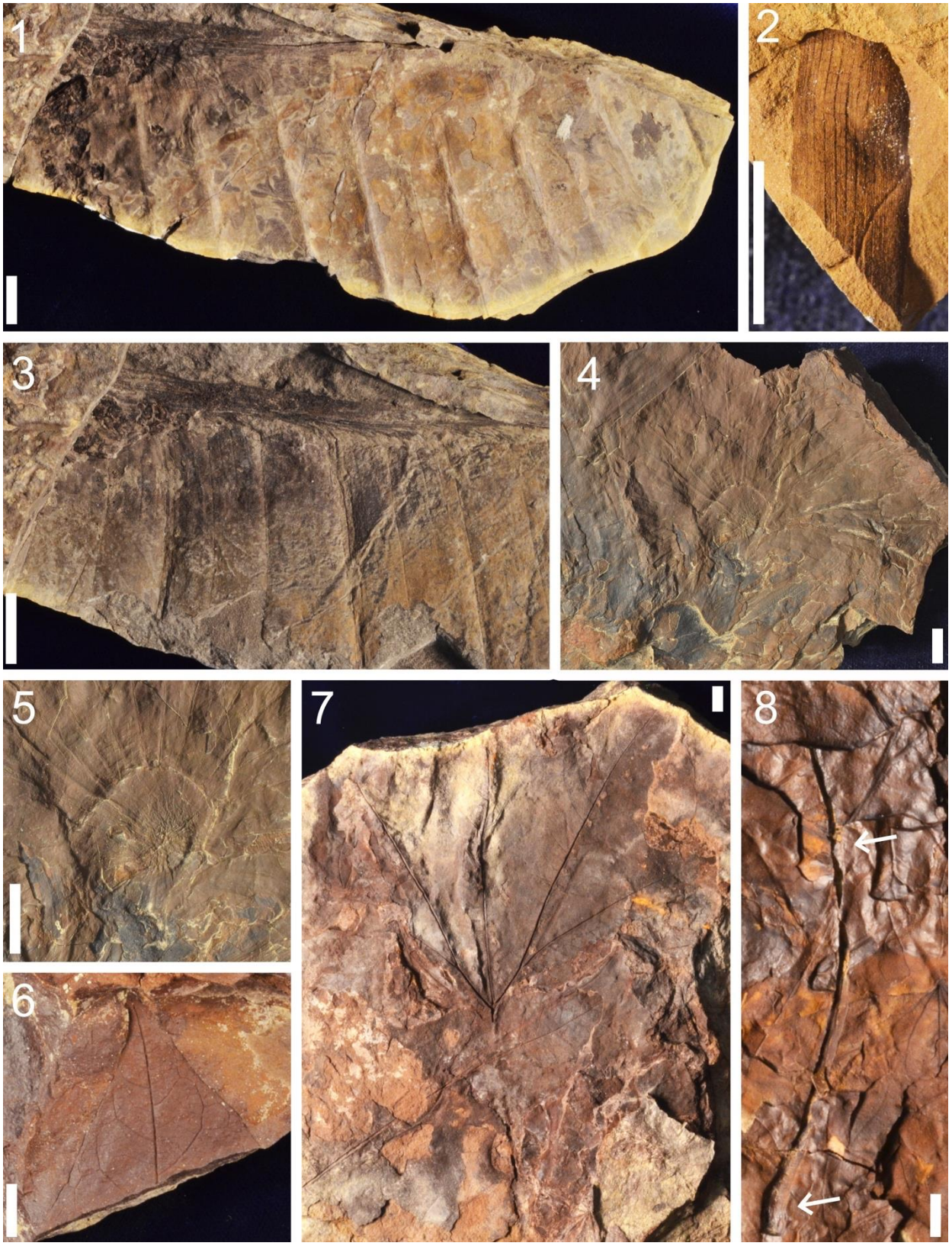
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Plate V

Fig. 1-2, 4 *Macginitiea* aff. *M. nobilis* (NEWBERRY) MANCHESTER

3. Foliar specimen showing more obtusely diverging palinactinodromous venation and strong lobation, scale 1 cm, YPM PB 169927
4. Foliar specimen showing more acute primary venation, scale 1 cm, USPC 1012-12076 (NUPB 732)
4. Foliar specimen showing strong lateral primary venation, lobes, and untoothed margin, scale 1 cm, USPC 1012-12077 (NUPB 733)

Fig. 3. *Macginicarpa* cf. *M. manchesteri* PIGG et STOCKEY, morphotype exemplar showing achenes and persistent styles, scale 1 cm, YPM PB 169907

Fig. 5-6, 10 *Platanus* sp.

5. Foliar specimen showing robust off-set palinactinodromous venation and tight basal lobes, scale 1 cm, USPC 367-3898. Previously figured as figure 11 in MCIVER & BASINGER 1999.
6. Foliar specimen showing broad lamina and basal lobes, scale 1 cm, USPC 367-3964
10. Counterpart of Figure 5 showing a more complete specimen, scale 1 cm, USPC 367-3898

Fig. 7-9 *Nordenskioeldia borealis* HEER

7. Morphotype exemplar, scale 1 cm, USPC 261-6334
8. Specimen showing ovoid follicles possibly disarticulated, scale 1 cm, USPC 111-4937
9. Top down view of follicle showing divided fruitlets, scale 1 cm, USPC 435-2726

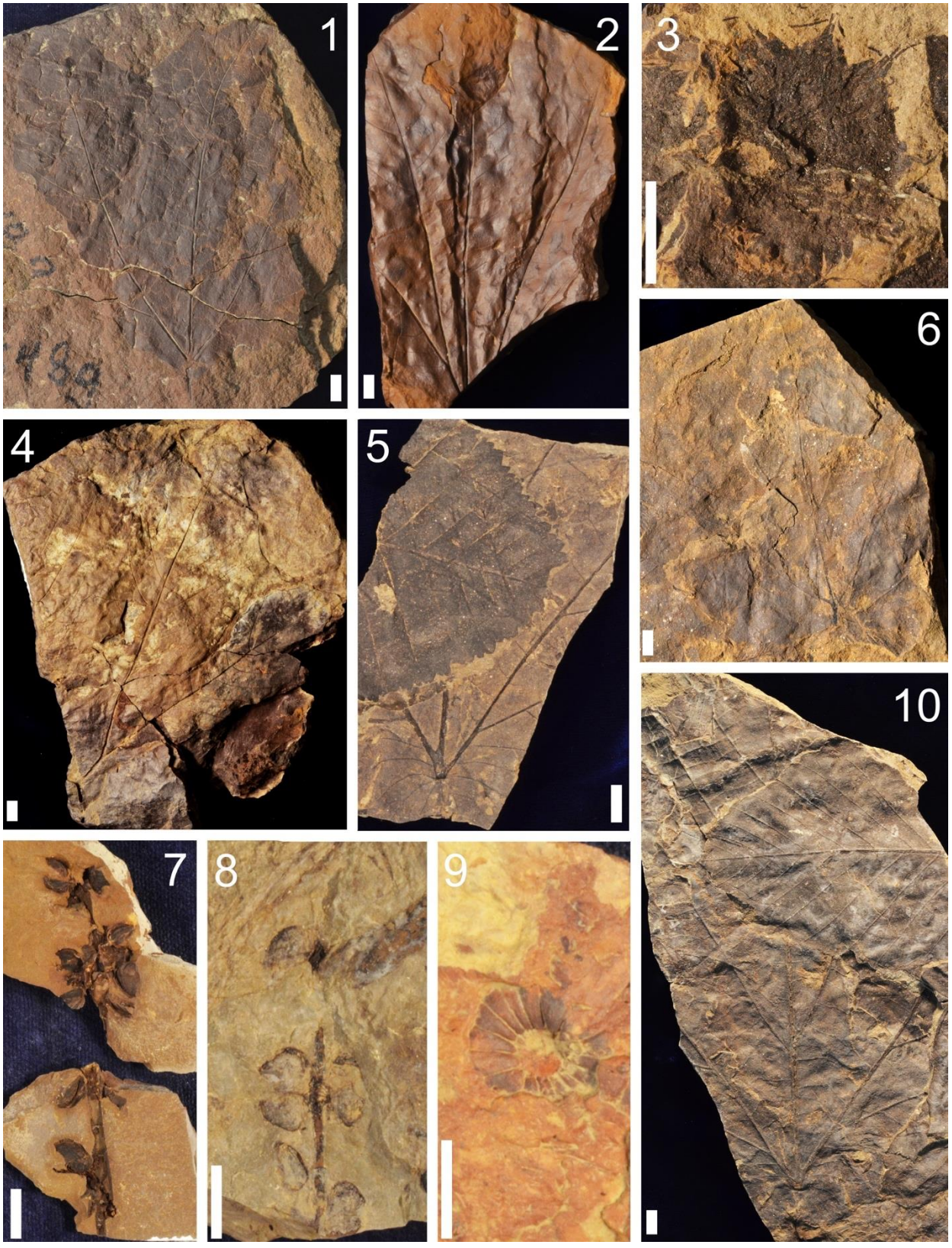
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Plate VI

Fig. 1-2. *Archeampelos* cf. *A. acerifolia* (NEWBERRY) MCIVER et BASINGER

1. Foliar specimen showing closer spaced well rounded teeth, scale 1 cm, USPC 179-4183
2. Close-up of USPC 436-2732.2 morphotype exemplar, arrows point to marginal glands, scale 1 mm

Fig. 3-4. *Trochodendroides arctica* (HEER) BERRY

3. Foliar specimen showing a broad reniform shape, scale 1 cm, USPC 22-1174
4. Foliar specimen showing an elliptic shape, scale 1 cm, USPC 105-4712

Fig. 5-6. *Nyssidium arcticum* (HEER) ILJINSKAJA

5. Infructescence with multiple helical follicles, scale 1 cm, USPC 367-3962
6. Morphotype exemplar showing probable seeds, scale 1 cm, USPC 261-6335

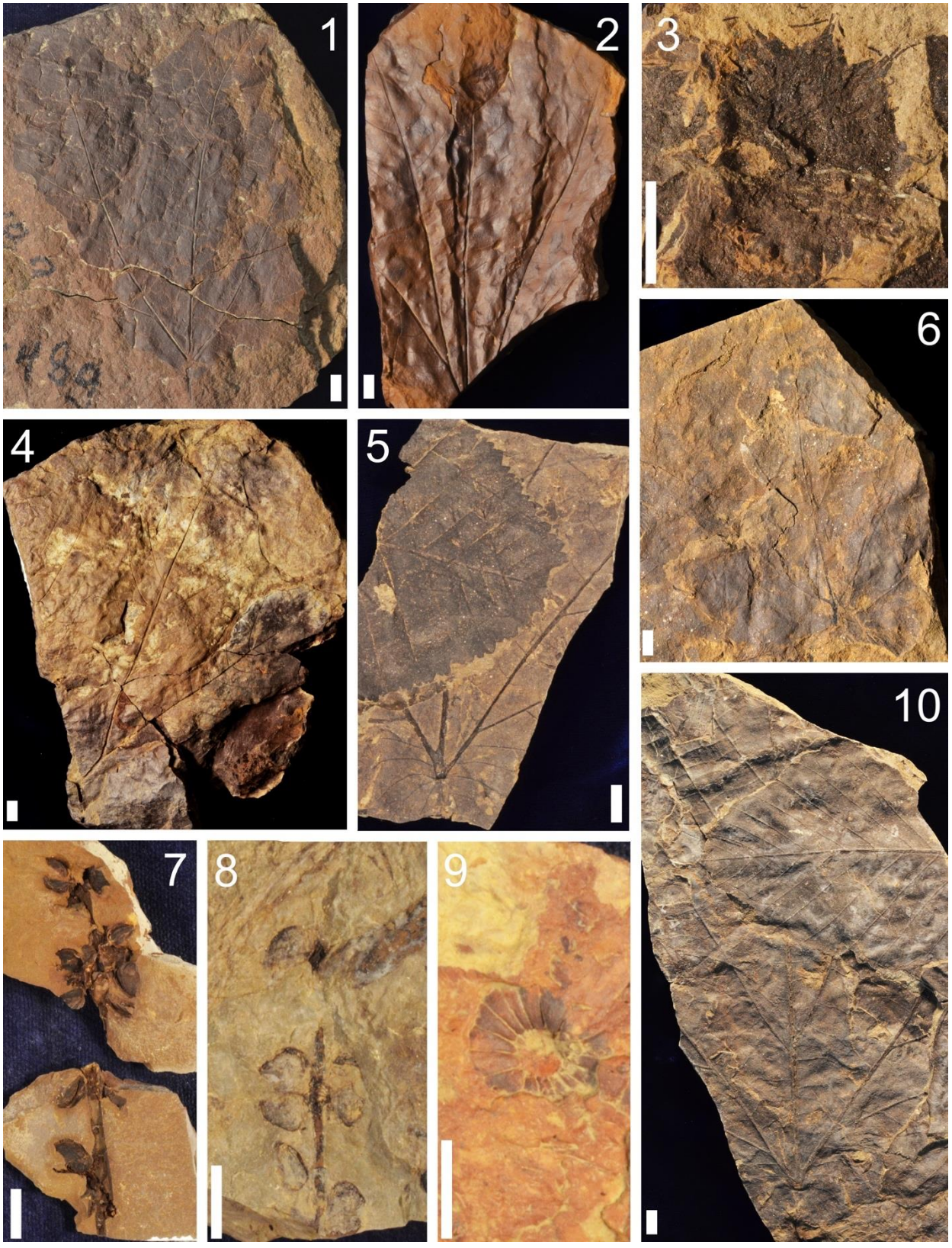
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Plate VII

Fig. 1. *Trochodendroides arctica* (HEER) BERRY, specimens showing a weakly crenate margin, scale 1 cm, USPC 111-4830

Fig. 2 & 5. *Trochodendroides crenulata* (HEER) KVAČEK, MANUM et BOULTER

2. Specimen showing exaggerated suprabasal acrodromous venation, scale 1 cm, USPC 111-4914
5. Specimen showing more robust crenate teeth and elliptic shape, scale 1 cm, USPC 111-4855

Fig. 3 & 6. *Trochodendroides richardsonii* (HEER) KRYSHTOFOVICH

3. Specimen showing broadly deltoid teeth, scale 1 cm, USPC170-4253
6. Specimen showing broad round teeth, scale 1 cm, USPC 111-4883

Fig. 4. *Trochodendroides curvidens* (HEER) GOLOVNEVA et BUDANTSEV, specimens with characteristic sharply acute teeth, scale 1 cm, USPC 166-4613

Fig. 7-8. gen. indet. sp. indet. Morphotype CAF-144

8. Possible bracts or seeds morphotype exemplar showing both triangular or rare chevron shape, scale 1 cm, USPC 200-4756
8. Specimen showing darkening along margin, scale 1 cm, USPC 111-4938

Fig. 9-10. *Vitiphyllum* cf. *V. sewardii* BOULTER et KVAČEK

9. Overlapping leaves. Lower specimen showing damaged apex and base, which causes specimen to appear similar to *Platanus or Platanites*, scale 1 cm, USPC 436-2734. Top specimen was previously figured as figure 16 in MCIVER & BASINGER 1999.
10. Specimen showing actinodromous venation and cordate base, scale 1 cm, USPC 367-3902

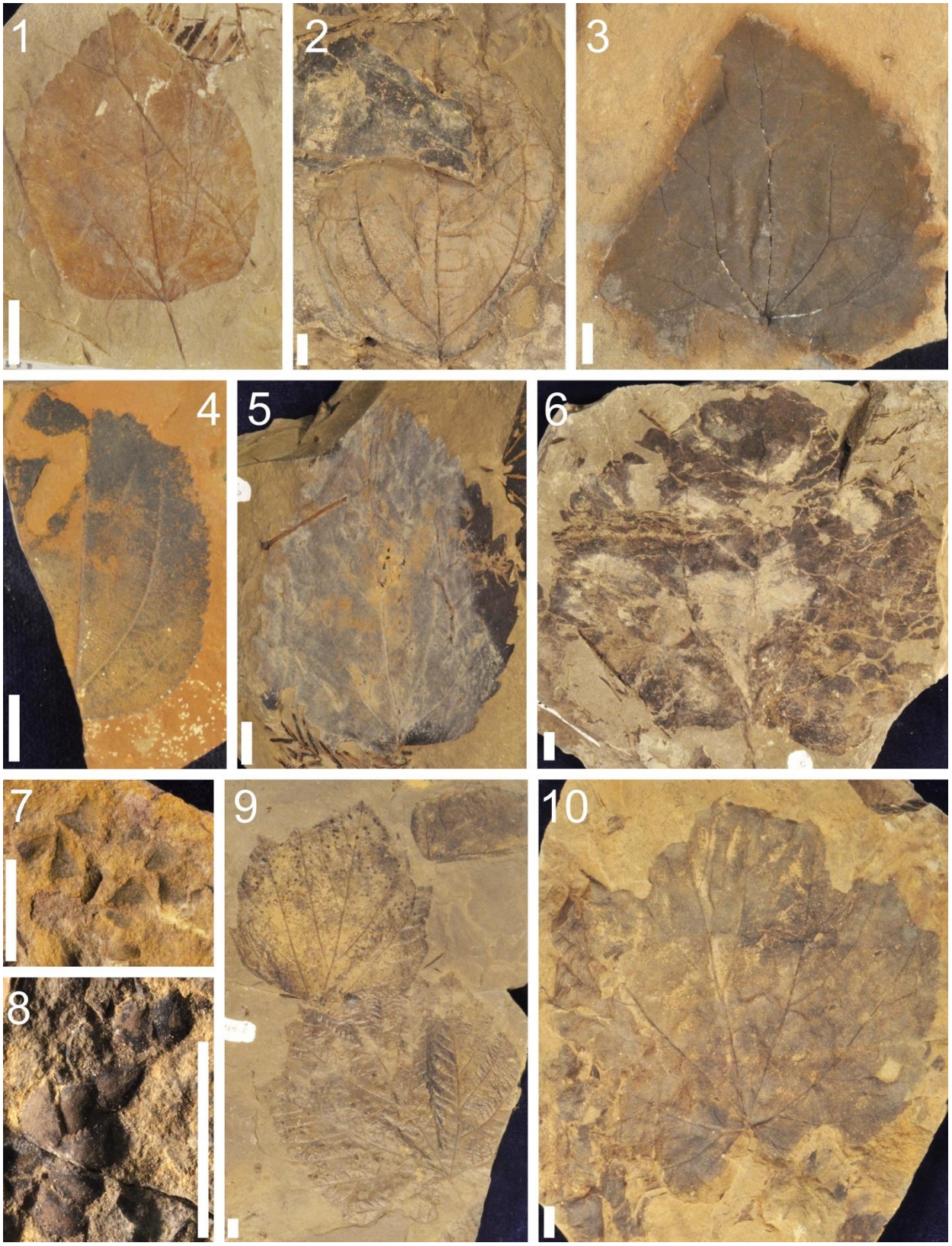
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Fig. 1. *Alnus* cf. *A. parvifolia* (BERRY) WOLFE et WEHR, leaf showing characteristic base and basal venation, scale 1 cm, USPC 259-3811

Fig. 2-3, 8. *Alnus* sp.

2. Mature seed infructescence morphotype exemplar showing ellipsoid shape, scale 1 cm, USPC 275-6138
3. Specimen showing a branching pair of infructescence, scale 1 cm, USPC 1014-12111 (NUPB 767)
8. Specimen showing a globose shape, scale 1 cm, USPC 275-6143

Fig. 4-5, 9. *Corylites hebridicus* SEWARD et HOLTTUM

4. Leaf with strongly cordate base, scale 1 cm, USPC 367-3897. Previously figured as figure 9 in MCIVER & BASINGER 1999.
5. Leaf showing the typically straight parallel secondary veins, scale 1 cm, USPC 367-3951
9. Leaf showing well defined dentate crenate teeth, scale 1 cm, USPC 200-4826

Fig. 6-7. cf. *Paracarpinus* sp.

6. Leaf showing strong parallel secondary veins, scale 1 cm, USPC 22-1189
7. Leaf fragment with well-preserved serrate dentition, scale 1 cm, USPC 435-2708. Previously figured by WEST et al., 2015, figure 3 as SF020.

Fig. 10. *Craspedodromophyllum* cf. *C. malmgrenii* (HEER) GOLOVNEVA, leaf showing an ovate shape, scale 1 cm, USPC 200-4818

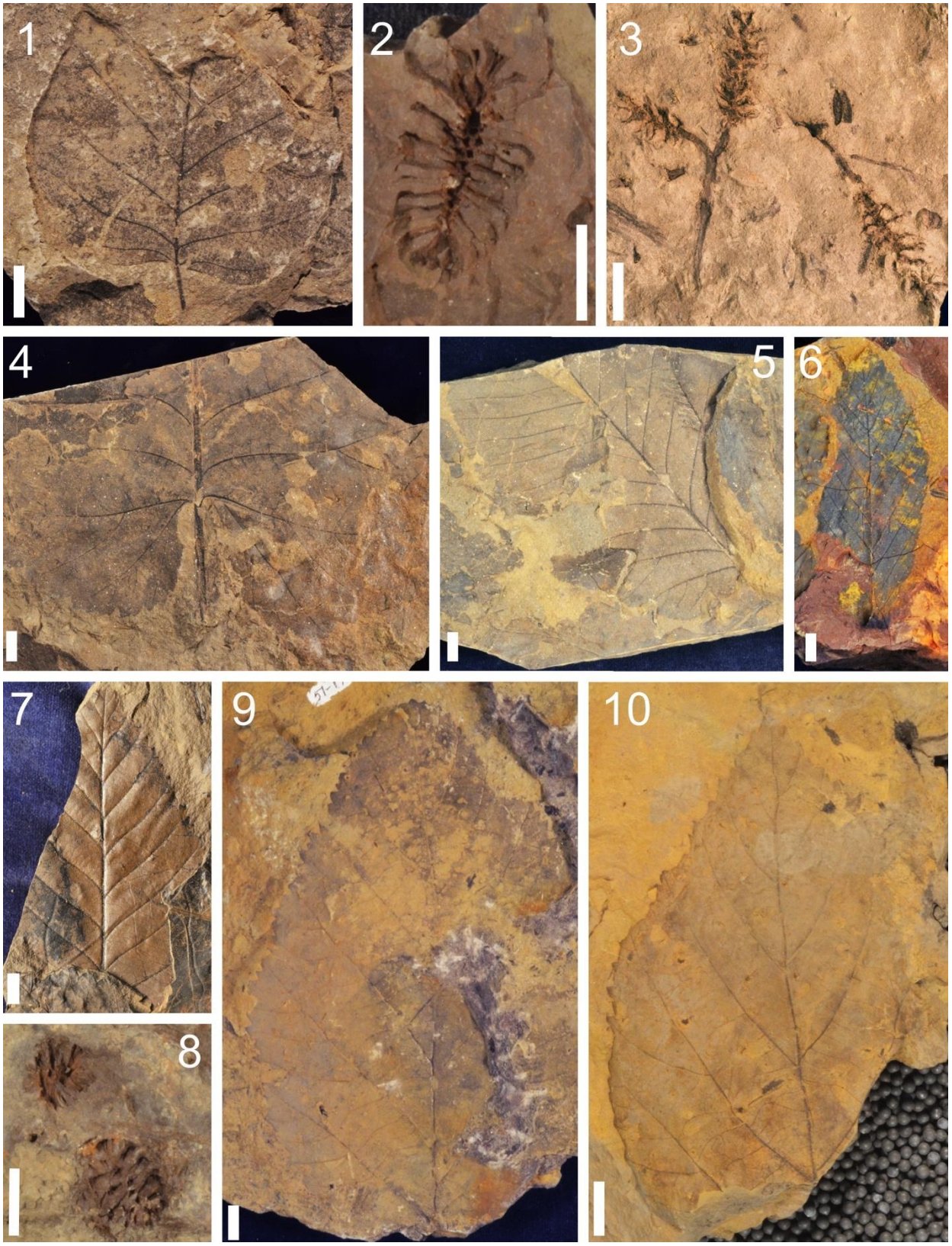
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Plate IX

Fig. 1. *Craspedodromophyllum* cf. *C. malmgrenii* (HEER) GOLOVNEVA, leaf showing compound agrophic veins and serrate margin, scale 1 cm, USPC 111-4864

Fig. 2-3. *Fagopsiphyllum* cf. *F. groenlandicum* (HEER) MANCHESTER

2. Leaf fragment showing serrate crenate teeth, scale 1 cm, USPC 111-4907
3. Leaf fragment with less robust dentition, scale 1 cm, USPC 105-4744

Fig. 4-6. *Ushia* cf. *U. olafsenii* (HEER) BOULTER et KVAČEK

4. Leaf with characteristic concavo-convex base and strong parallel tertiary venation, scale 1 cm, USPC 111-6167. Previously figured as figure 4 in MCIVER & BASINGER 1999.
5. Leaf with larger deltoid teeth, scale 1 cm, USPC 105-4727
6. Leaf with a decurrent base, scale 1 cm, USPC 111-6153

Fig. 7-8. cf. '*Carya*' *antiquorum* NEWBERRY

7. Leaf showing secondary venation curving sharply within margin, scale 1 cm, USPC 111-4901
8. Leaf with disorderly secondary venation along primary vein, scale 1 cm, USPC 175-4112

Fig. 9-10. *Comptonia* sp.

9. Morphotype exemplar specimen with cuneate base, scale 1 cm, USPC 164-4272
10. Leaf with more falcate lobes and partially complete apex, scale 1 cm, USPC 164-4272

Fig. 11. cf. *Crataegus* sp. 1, leaf with concave base, scale 1 cm, USPC 753-2076

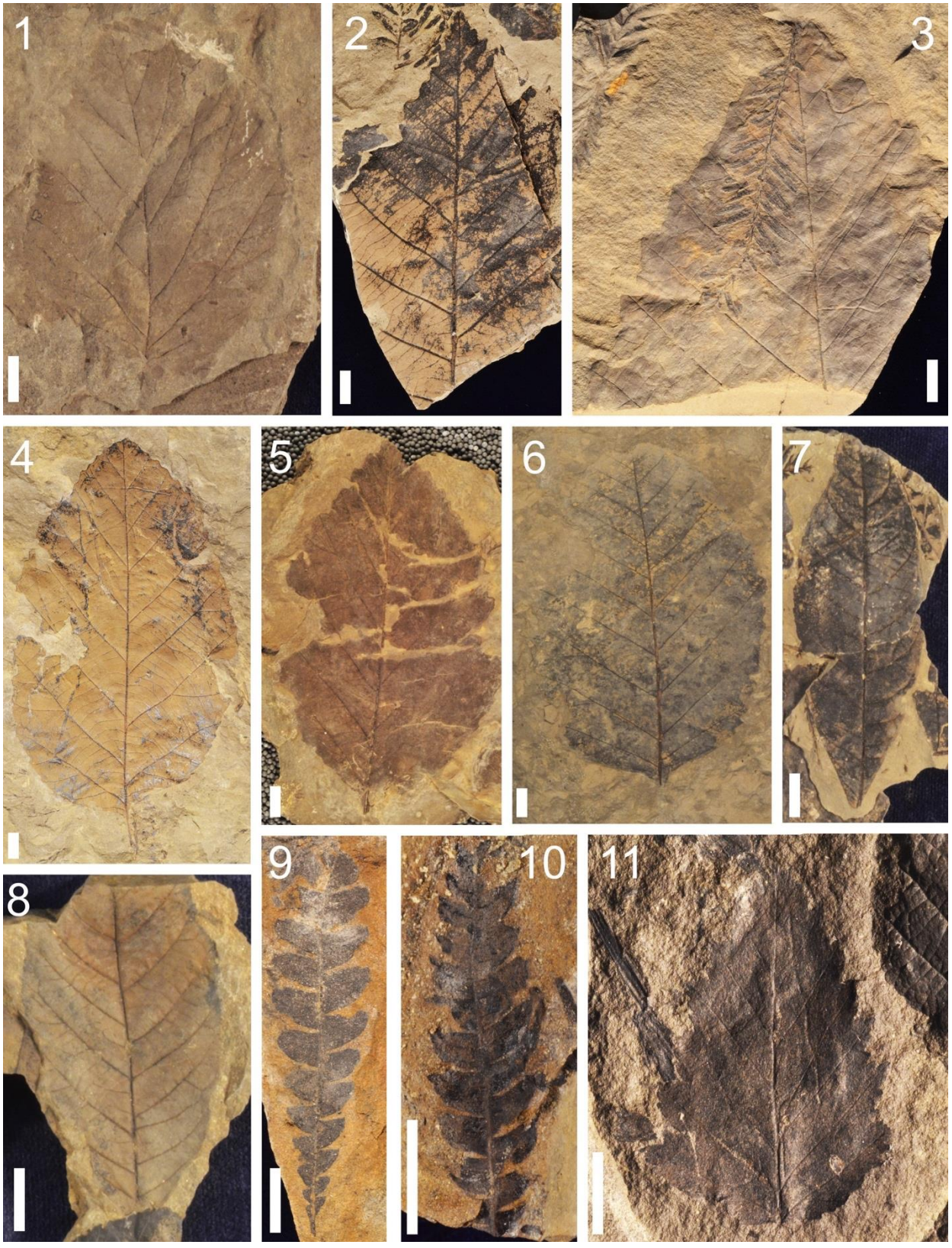
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Plate X

Fig. 1-2. cf. *Crataegus* sp. 1

1. Leaf fragment showing typical compound teeth of cf. *Crataegus* sp. 1, scale 1 cm, USPC 753-2086
2. Leaf showing more exaggerated compound teeth, scale 1 cm, USPC 753-2080

Fig. 3-5, 8. *Ulmus ulmifolia* (SCHLOEMER-JÄGER) BUDANTSEV

3. Leaf showing serrately crenate teeth, scale 1 cm, USPC 200-4779
4. Leaf with cordate base, scale 1 cm, USPC 111-4888. Previously figured as figure 15 in MCIVER & BASINGER 1999.
5. Leaf fragment with acuminate apex, scale 1 cm, USPC 111-4957
8. Leaf with ovate shape and broad serrate teeth, scale 1 cm, USPC 435-2723. Previously figured by WEST et al., 2015, figure 3 as SF008.

Fig. 6-7, 9-10. *Aesculus longipedunculus* SCHLOEMER-JÄGER

6. Leaf with damaged acute apex, scale 1 cm, USPC 105-4715
7. Leaf with well-ordered secondary venation that terminates at margin, scale 1 cm, USPC 200-4824. Previously figured as figure 13 in MCIVER & BASINGER 1999.
9. Leaf with well-preserved robust primary and secondary venation and finely serrate margin, scale 1 cm, USPC 422-3866. Previously figured by WEST et al., 2015, figure 5 as STF015.
10. Close-up of USPC 111-4900 showing semicraspedodromous secondary venation looping tightly near the margin, scale 1 cm

Fig. 11. *Averrhoites* cf. *A. affinis* (NEWBERRY) HICKEY, fragmentary leaf, scale 1 cm, USPC 177-4146

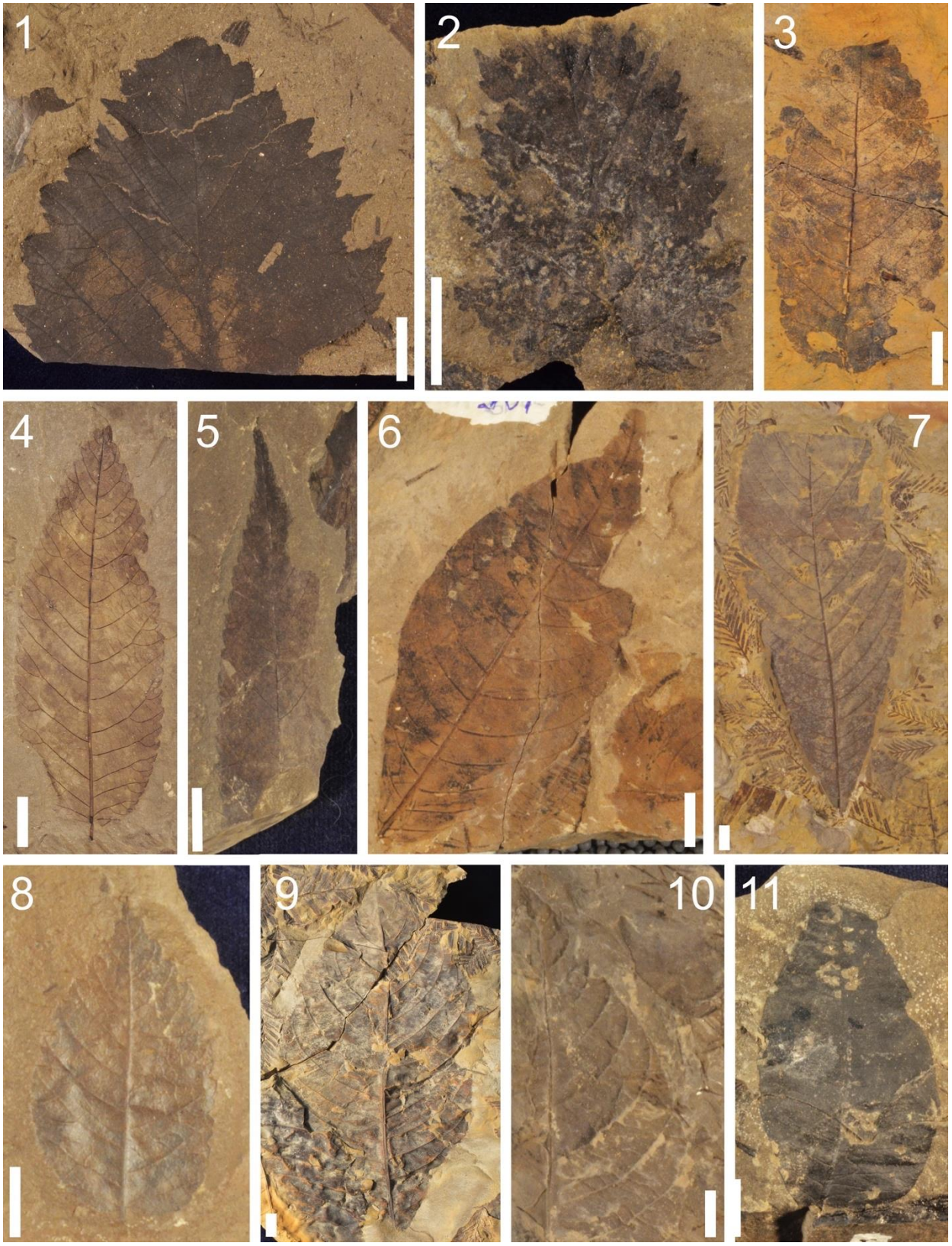
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Plate XI

Fig. 1. *Averrhoites* cf. *A. affinis* (NEWBERRY) HICKEY, folded over leaf with acute apex, scale 1 cm, YPM PB 169846

Fig. 2-3, 6-8. *Quereuxia angulata* (NEWBERRY) KRYSHTOFOVICH

2. Leaf with serrate teeth and visible primary and secondary venation, scale 1 cm, USPC 360-3893
3. Rhizome with nodes and rhizome leaves, scale 1 cm, USPC 362-3927
6. Rhizome with branching roots, scale 1 cm, USPC 360-3908
7. Rhizome with finer curving rootlets, scale 1 cm, USPC 360-3911
8. Morphotype exemplar, compound leaf, scale 1 cm, USPC 191-3967

Fig. 4. aff. *Celastrinites* sp., overlapping leaves with possible brochidodromous or craspedodromous venation, scale 1 cm, USPC 261-6113

Fig. 5. *Macclintockia* sp., morphotype exemplar, scale 1 cm, USPC 168-4270

Fig. 9-11. gen. indet. sp. indet. CAF-016

9. Leaf with secondary venation that alternates along primary vein, scale 1 cm, USPC 363-3905
10. Leaf showing obovate shape and finely serrate margin, scale 1 cm, USPC 436-2756
11. Leaf with cuneate base and petiole, scale 1 cm, USPC 442-2816. Previously figured by WEST et al. 2015, figure 4 as SL007.

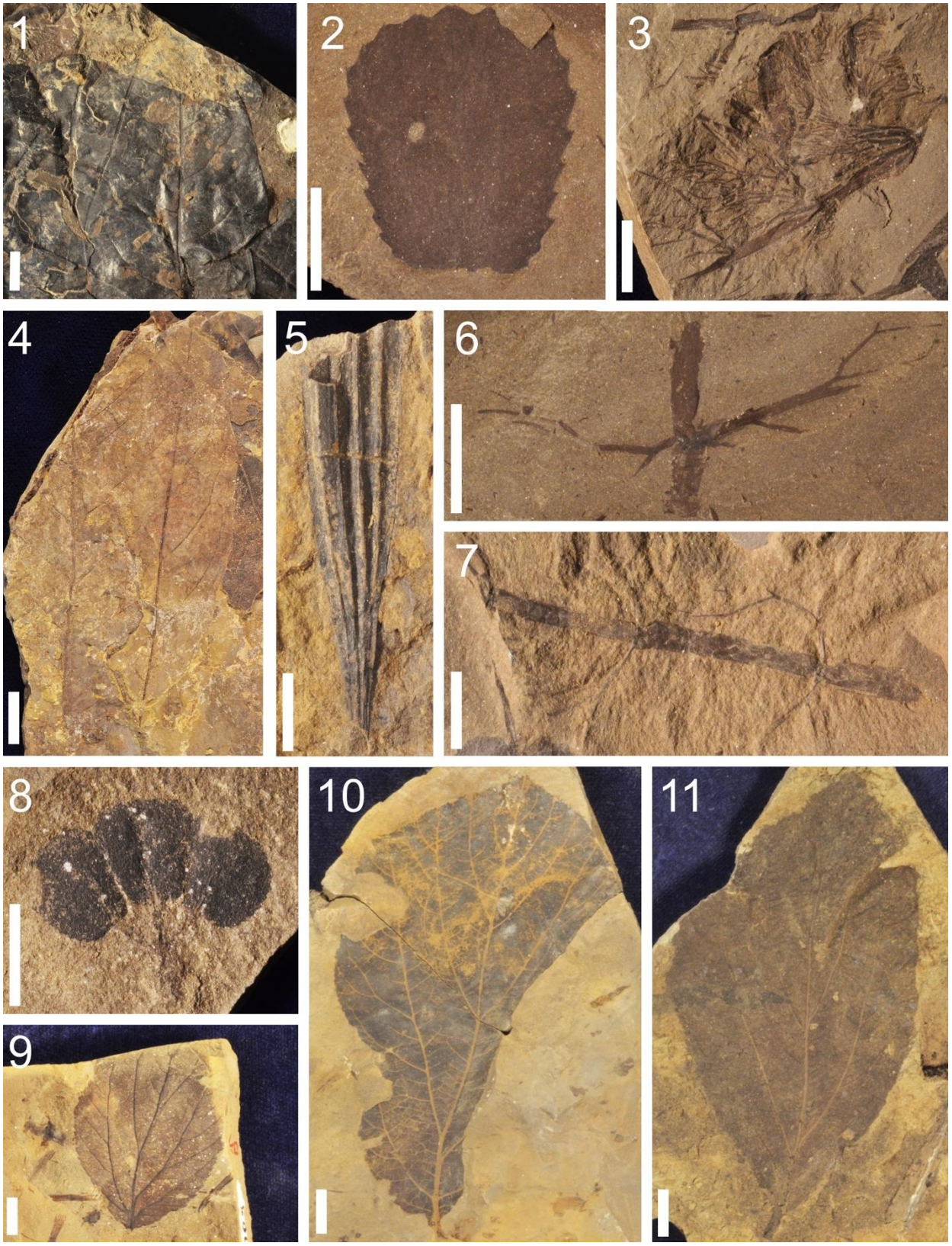
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Plate XII

Fig. 1. gen. indet. sp. indet. Morphotype CAF-073, leaf showing semicraspedodromous venation, scale 1 cm, USPC 175-4118

Fig. 2-3. gen. indet. sp. indet. Morphotype CAF-134

2. Morphotype exemplar specimen, scale 1 cm, USPC 436-2733
3. Additional specimens found on morphotype exemplar sample, arrows denote basal actinodromous of fragmentary leaves, scale 1 cm, USPC 436-2733

Fig. 4-5, 7. gen. indet. sp. indet. Morphotype CAF-086

4. Infructescence morphotype exemplar, arrow points at tightly grouped pedicels, scale 1 cm, USPC 6-498. Previously figured as figure 17 in McIver & Basinger 1999.
5. Infructescence showing additional detail of preserved follicles with longitudinal striations, scale 1 cm, USPC 435-2697
7. Infructescence showing a branched pair of pedicel-bearing follicles, scale 1 cm, USPC 6-6214

Fig. 6. gen. indet. sp. indet. Morphotype CAF-123, morphotype exemplar, scale 1 cm, YPM PB 169888

Fig. 8. gen. indet. sp. indet. Morphotype CAF-124, morphotype exemplar, scale 1 cm, USPC 111-4922

Fig. 9. gen. indet. sp. indet. Morphotype CAF-130, leaf showing suprabasal actinodromous venation and serrate teeth only in the upper third of the lamina, scale 1 cm, USPC 200-4771

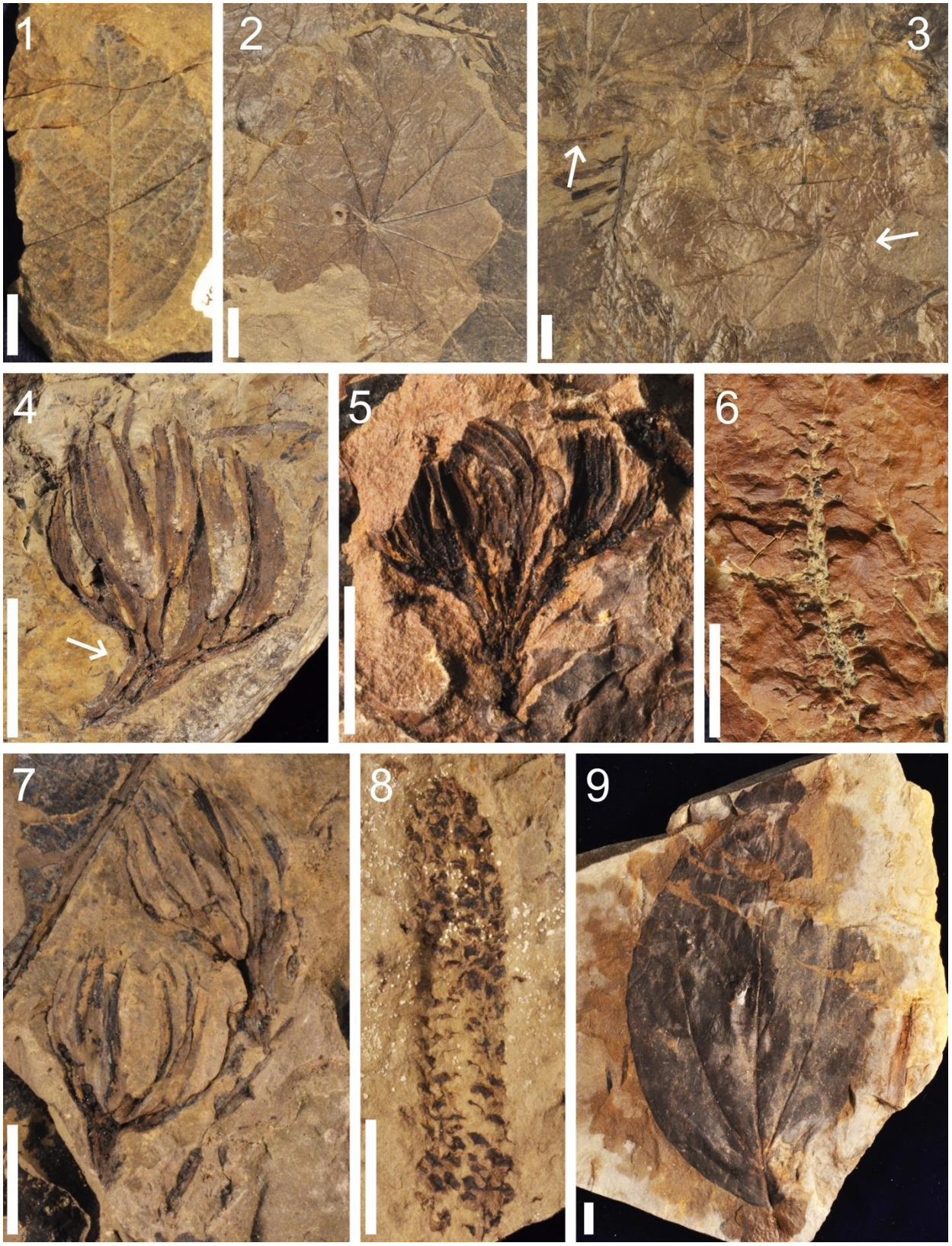
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Plate XIII

Fig. 1. gen. indet. sp. indet. Morphotype CAF-137, morphotype exemplar, scale 1 cm, USPC 438-2786

Fig. 2. gen. indet. sp. indet. Morphotype CAF-147, morphotype exemplar, scale 1 cm, USPC 261-6317

Fig. 3 & 6. gen. indet. sp. indet. Morphotype CAF-093

3. Morphotype exemplar, scale 1 cm, USPC 261-6115
6. Close-up of USPC 261-6115 showing possible exocarp, scale 1 cm

Fig. 4. gen. indet. sp. indet. Morphotype CAF-146, morphotype exemplar, scale 1 cm, USPC 111-4924

Fig. 5. gen. indet. sp. indet. Morphotype CAF-138, morphotype exemplar, scale 1 cm, USPC 22-1217

Fig. 7-8. gen. indet. sp. indet. Morphotype CAF-140

7. Possible short shoot or spur shoot, scale 5 mm, USPC 436-2773
8. Morphotype exemplar, scale 1 cm, USPC 436-2747

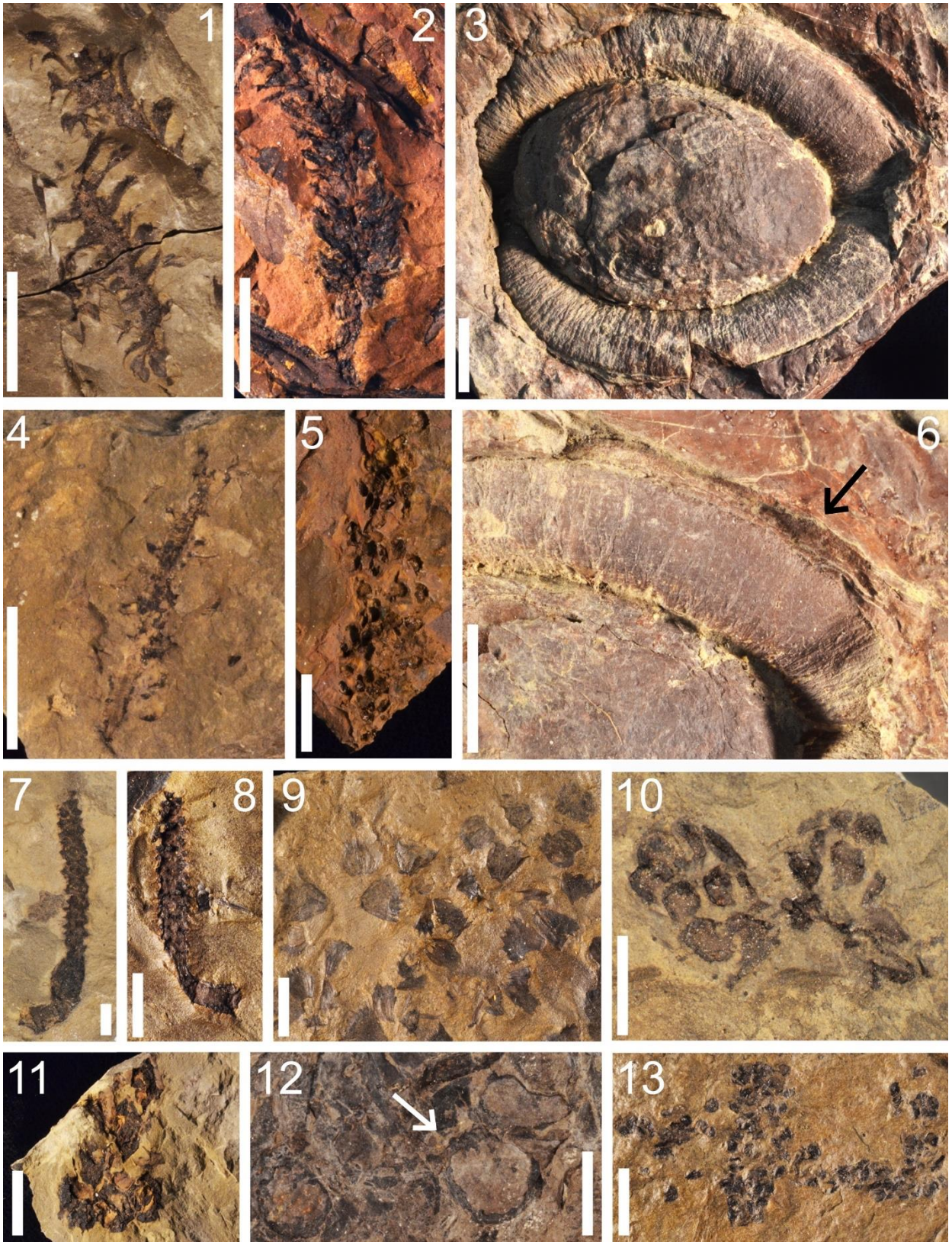
Fig. 9. gen. indet. sp. indet. Morphotype CAF-141, morphotype exemplar, scale 1 cm, USPC 436-2773

Fig. 10 & 13. gen. indet. sp. indet. Morphotype CAF-142

10. Seeds showing overlapping organization, scale 5 mm, USPC 436-2776
13. Morphotype exemplar showing apparent alignment along a central axis, scale 1 cm, USPC 436-2776

Fig. 11. gen. indet. sp. indet. Morphotype CAF-145, woody fruits or fertile scale, morphotype exemplar, scale 1 cm, USPC 111-4920

Fig. 12. gen. indet. sp. indet. Morphotype CAF-143, morphotype exemplar, scale 1 cm, USPC 169-3981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4. HIGH ARCTIC FOREST DIVERSITY AND FLORISTIC CHANGE DURING EARLY EOCENE HYPERTHERMAL EVENTS

This chapter was submitted to the journal *Science* and adheres to the style and format required to be published by that journal, and will be published as: WEST, C.K., GREENWOOD, D.R., SUDERMANN, M., REINHARDT, L., GALLOWAY, J.M., & BASINGER, J.F. (submitted). High Arctic forest diversity and floristic change during early Eocene hyperthermal events.

ABSTRACT: The modern Arctic is characterized by low floral diversity and a cold dry climate; however, the Arctic of the early Eocene was much warmer and wetter, yet the forest diversity for Arctic Eocene ecosystems is typically described as low and homogenous, an idea that remains relatively untested. Reported here are the first quantitative megafloral diversity estimates from Stenkul Fiord, Ellesmere Island, Canada, utilizing two census-sampled collections coupled with horizon-specific palynological analysis. Recent U-Pb geochronology place the fossil collections stratigraphically near the PETM and ETM2 hyperthermal events of the early Eocene, a time when warm equable climates allowed temperate and tropical plant taxa to survive at high northern latitudes. Results show that the early Eocene paleoarctic forests supported diverse ecosystems with floral diversity similar to modern mid-latitude broadleaf forests from North America, but overall floral diversity was restricted as a result of photic seasonality. Furthermore, these ecosystems experienced floristic change probably related to the transient hyperthermal events.

ONE SENTENCE SUMMARY: Fossil leaves and pollen show early Eocene high-latitude Arctic forests were as diverse as modern temperate forests.

4.1 MAIN TEXT:

The causes of the modern latitudinal diversity gradient (LDG) are a longstanding problem in ecology (*1–2*). Temperature has been proposed as the primary driver of the modern LDG, although other hypotheses, with various causal mechanisms (e.g., precipitation, insolation,

seasonality, biogeographical history, and biological interactions), have been suggested as constraints or drivers of diversity in the extratropics (i.e., the mid- and high-latitudes) (*1–3*). Tropical-style plant diversity extended well into the mid-latitudes in the Eocene, as evidenced by fossil data and probably resulting from floral immigration due to the flattening of the latitudinal temperature gradient (*1*, *4–8*). These hyper-diverse Eocene mid-latitude sites imply temperature or thermal seasonality as a primary driver of diversity (*1*, *4–7*). However, if temperature had an overriding influence on diversification, then diversity should have increased in polar regions during the warming trend of the late Paleocene–early Eocene, a trend previously documented in the tropics (*2–3*, *9*).

The early Eocene Arctic environments have been historically viewed as low diversity taxodioid Cupressaceae swamps; however, the warm global temperatures of the early Eocene allowed plant taxa restricted to warm temperate and tropical climates to grow at both mid- and high latitudes (*4–5*, *10–12*). The diversity of early Eocene paleoarctic forests has rarely been tested or quantified for comparison to contemporaneous fossil flora localities from both the mid- and low latitudes in North America (*6–7*, *9*, *12*). Prior studies have either focused on assessing taxonomic richness from museum collections, which may suffer from collector's bias (*10*, *12*), or have assessed diversity using time-averaged coal-facies pollen assemblages where key taxa were not resolved to species (*11*).

Fossils for this study were sampled from measured sections at Stenkul Fiord (SKF), Ellesmere Island, Nunavut, Canada, located at approximately 77°N, 83°W, with an approximate Eocene paleolatitude of ~74–76°N (*14–16*). Fossil megaflora were quarried from silt and mudstone fluvial deposits of the late Paleocene to early Eocene Margaret Formation of the Eureka Sound Group (*17–18*). Palynological analysis was conducted on stratigraphically constrained sediment samples from the fossil megaflora horizons, and stratigraphically close coal horizons to allow comparability with prior studies.

Previous biostratigraphic palynological analyses and associated vertebrate fossils have indicated a late Paleocene to early Eocene age for the sediments at SKF (*14*, *16*, *19*). Prior U-Pb analyses of local volcanic ashes from the western shore at SKF have provided an age of 53.7 Ma ± 0.6 Ma, which captures the Eocene Thermal Maximum 2 (ETM2) hyperthermal event (*20–21*) in sections S1 and S3 (Fig. 4.1). Recent analyses have found evidence of the Paleocene-Eocene Thermal Maximum (PETM) event in stratigraphic section S1 (21–22), and section S1 is interpreted as stratigraphically younger than section S5 (*17*, *21*) (Fig. 4.1).

The fossil leaf and palynofloras were sampled from a horizon in section S5 that, based on recent geological mapping, occurs stratigraphically below the PETM (*21*), and from a horizon in section S3 that occurs stratigraphically above the ETM2 ash layer (*19*) (Fig. 4.1). Totals of ~375 and ~365 plant megafossil specimens (Table S1) were recovered from localities USPC-1005 and USPC-1014, respectively. Megafossils were sorted into 21 distinct morphotypes (Fig. 4.2) based on an existing framework (*12*); fifteen morphotypes are broad-leaf angiosperms, and represent 317 and 207 specimens from the two localities, respectively. A minimum count of 400 pollen and spore specimens per sample were counted (Table S2), and 92 taxa were identified from the four mudstone and coal samples. Within-sample richness of pollen and spores for the leaf-bearing mudstone samples was 32 and 39 taxa for the pre-PETM and post-ETM2 samples, respectively.

Diversity was assessed using interpolation- and extrapolation-based rarefaction, which depicts species diversity as Hill numbers (Fig. S1-S2, Table S3-S8), theoretical numbers that equate to the effective number of species, as well as sample coverage (Fig. S3), and sample completeness (*23–25*). Simpson's Diversity, the Shannon Diversity Index and Evenness were also calculated (Table S9). The curves were derived using census-count abundance data of the dicot compression fossils and the palynoflora. Both leaf and pollen and spore data were rarified against modern vegetation samples from the mid-latitudes of North America for diversity comparisons, similar to previous studies (*11*).

Sample completeness was assessed for both census leaf data and pollen and spore counts and demonstrates that each fossil locality was sufficiently well sampled for diversity analysis (Fig. 4.3). Extrapolation- and interpolation-rarefaction analyses for abundance data of the census leaf data and pollen and spore counts, when compared against modern forest data, show that SKF was similar in diversity to modern North American mid-latitude broadleaf forests (Fig. 4.3).

Rarefaction analysis confirms interpretations from a previous study that suggested the early Eocene paleoarctic forests of Canada were of similar diversity to modern mid-latitude broadleaf forests (*11*). However, the diversity contained in the pollen assemblages from the present study were considerably more diverse than found in a previous study at SKF, both when pooled and from within-sample richness (*11*). This may be in part because pollen and spore taxa were identified to species level rather than higher taxonomic classifications. The floral diversity of the fossil horizon stratigraphically below the PETM does not appear to differ from that of the locality stratigraphically above ETM2.

Previous studies demonstrated that terrestrial plants responded to hyperthermal events at mid-latitudes (e.g. Big Horn Basin, Wyoming), where during the PETM some plant taxa either originated, became locally extirpated, or eventually recolonized during or following the hyperthermal (*26*). Vegetation change associated with hyperthermal initiation and recovery has also been documented using palynological assemblages from marine sediment cores from the Arctic Basin (*27–28*). Extirpation and origination may also be observable in the megafossil record, as specific taxa disappear (e.g. *Ulmus*) or originate (e.g. *Macginitiea*) in the SKF fossil record, stratigraphically above the ETM2, although taphonomic and depositional bias cannot be discounted. The middle Eocene high Arctic megafloral record suggests that *Ulmus* does not return to the Arctic, as it is conspicuously absent from the many middle Eocene megafossil collections from Axel Heiberg (*10*). *Ulmus* pollen does, however, occur as a minor constituent

(<1%) of the mid-Ecoene terrestrial microfossil record (*29–30*). *Ulmus* is, however, also a minor component of the palynoflora in the pre-PETM record even as megafossils are abundant.

Mean annual temperature (MAT) for SKF was previously reconstructed from leaf physiognomy using the Climate Leaf Analysis Multivariate Program (CLAMP) and leaf margin analysis (LMA), with an estimated range of 8.5–12.7 ºC using a multi-proxy approach (*31*). Mean annual precipitation (MAP) was previously reconstructed for SKF using leaf area analysis (LAA) and estimated to be >150 cm/yr (*31*). These estimates, combined with palm or palm-like palynomorphs, and thermophilic fauna, indicate the Canadian paleoarctic experienced warm non-freezing winter temperatures (*14, 24, 28*). Falkland and McAbee, two upland early Eocene fossil plant localities from British Columbia, Canada, which are considered to be hyper-diverse, have a reconstructed MAT of ≈ 8–14 ºC and MAP of ≈ 82–146 cm/yr (*5, 32*). These climate estimates are similar to MAT and MAP reconstructed for multiple sites in the high Arctic (*31*).

It has been previously suggested that photic seasonality in the high Arctic may not have been a major factor restricting biodiversity (*11*); however, climatic similarity between the mid- and high latitude fossil sites predicts that floral diversity of the paleoarctic would have been higher during the early Eocene. The new data presented here instead shows that floral diversity was lower than predicted, and likely was constrained as a result of the seasonal photic regime. Thus, insolation and photic seasonality played a strong role at high latitudes, and reduced plant productivity and resulting abiotic stress likely precluded additional floral taxa from exploiting the high Arctic, which limited the influence of biogeographical controls such as speciation, extinction, and dispersal. These data suggest that neither temperature nor dispersal were influential drivers of high latitude floral diversity in the early Eocene—factors that exerted greater influence in the mid-latitudes.

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Supporting material and methods for this chapter, found in Appendix C, include:

Material and Methods

Paleobotany collection methods.

Palynology.

Diversity analyses.

Geological section measurements.

Fig S1–S3

Table S1–S9

References (34–50)

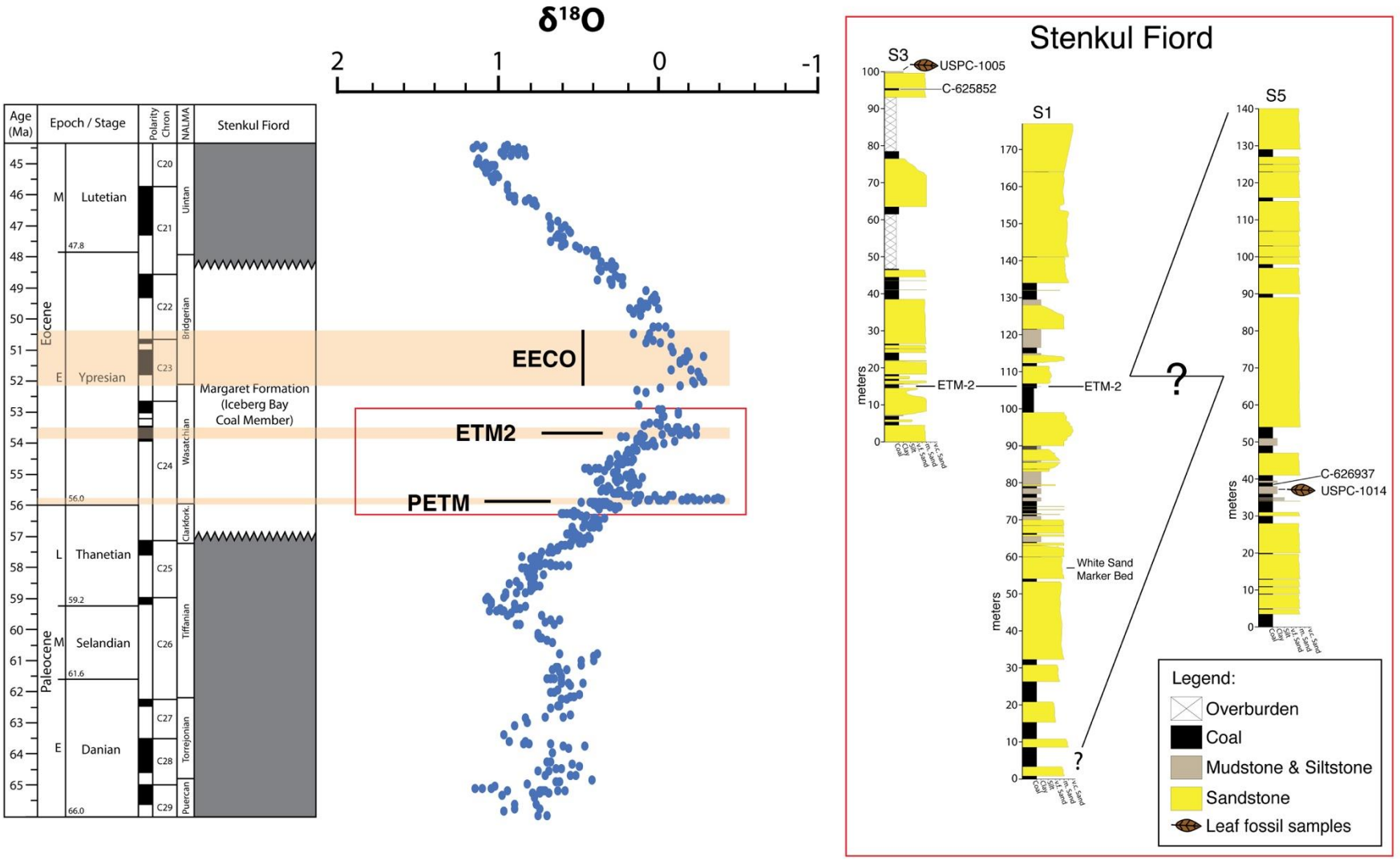


Fig. 4.1 Simplified geological lithostratigraphy sections. Section S1 and S3 are located on the western bank of Stenkul Fiord on southern Ellesmere Island, and section S5 is located on the eastern bank of Stenkul Fiord. Sections S1 and S5 are correlated based on prior U-Pb analyses of local ash layers, and provide an age of 53.7 Ma ± 0.6 Ma and captures the ETM2 (*20–21*). Recent analyses have found evidence of the Paleocene-Eocene Thermal Maximum (PETM) event in stratigraphic section S1 (21–22), and section S5 is interpreted late Paleocene in age and stratigraphically older than section S1 (*17, 21*). Sections are correlated to existing isotopic (red box) marine core data (*33*) that represent the major negative isotope excursions of the early Eocene.

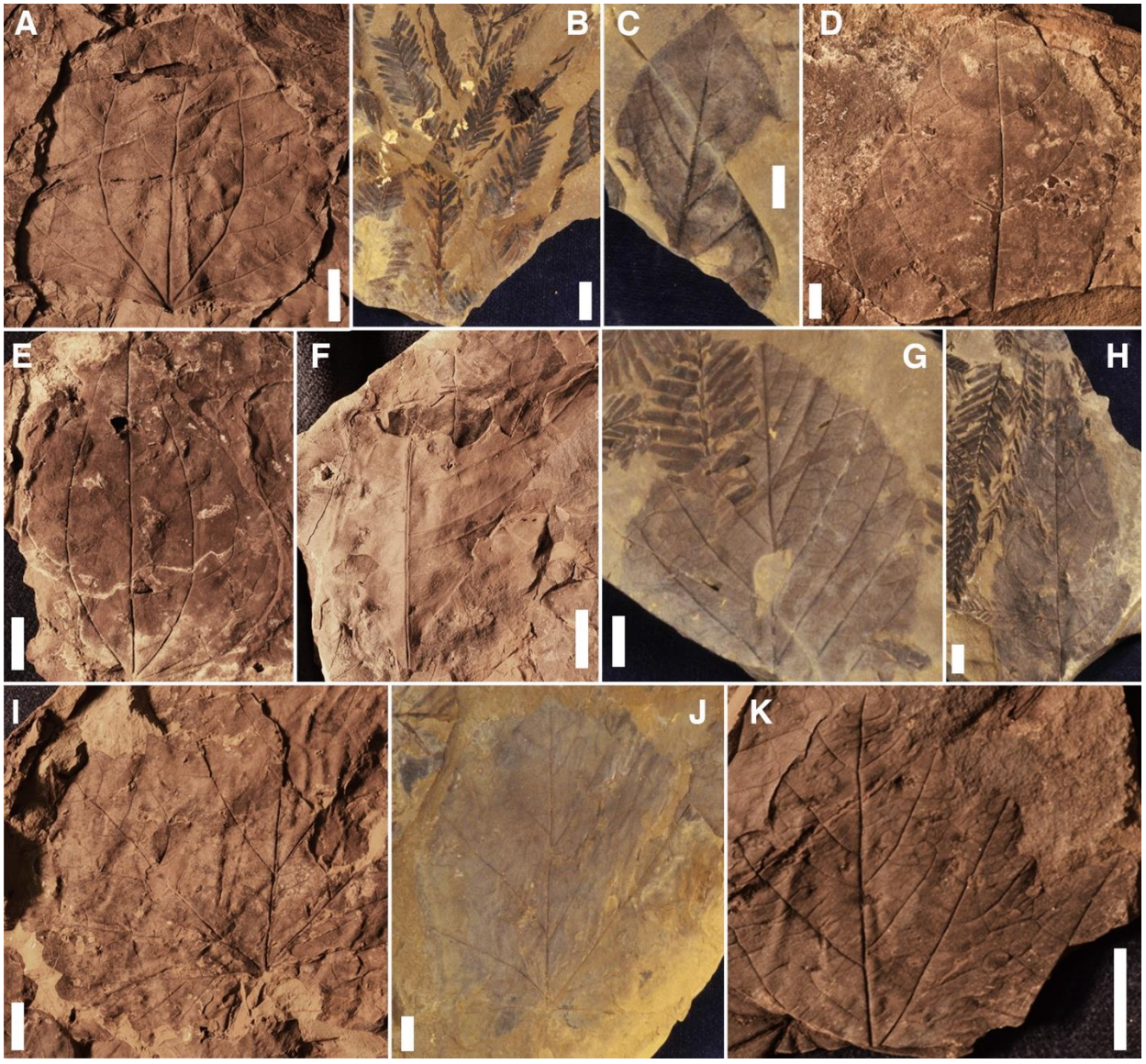
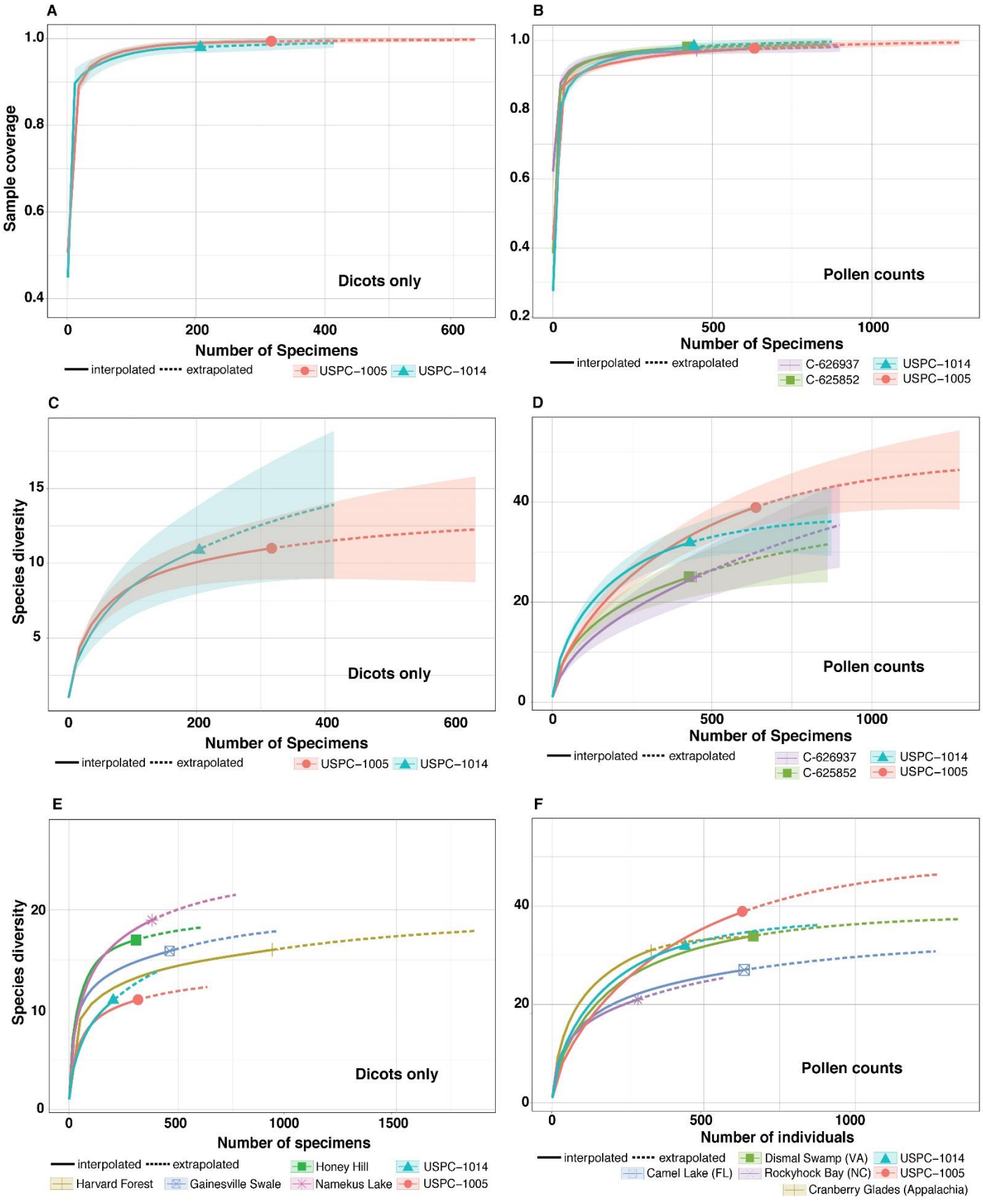


Fig. 4.2. Examples of fossil megaflora collected from localities USPC-1005 and USPC-1014 at Stenkul Fiord. (A, E) *Trochodendroides* sp. morphotypes were lumped in a conservative approach (B) *Metasequoia occidentalis* (C) Unidentified angiosperm leaf (D) leaf lobe apex of *Macginitiea* sp. (F) leaf base of *Aesculus* sp. (G) *Alnus* sp. (H) *Ulmus* sp. (I) basal lobe of *Archeampelos* sp. (J) *Vitiphyllum* sp. (K) leaf apex of *Archeampelos* sp. Leaf identities based on a systematic morphotype framework previously established for Ellesmere Island (*12*). All scales = 1 cm.


A
Sample coverage
1.0
0.8
0.6
0.4
Dicots only
0
200
400
600
Number of Specimens
interpolated
extrapolated
USPC−1005
USPC−1014
B
1.0
0.8
0.6
0.4
0.2
Pollen counts
0
500
1000
Number of Specimens
interpolated
extrapolated
C-626937
C-625852
USPC−1014
USPC−1005
C
Species diversity
15
10
5
Dicots only
0
200
400
600
Number of Specimens
interpolated
extrapolated
USPC−1005
USPC−1014
D
40
20
0
Pollen counts
0
500
1000
Number of Specimens
interpolated
extrapolated
C-626937
C-625852
USPC−1014
USPC−1005
E
Species diversity
20
10
0
Dicots only
0
500
1000
1500
Number of specimens
interpolated
extrapolated
Honey Hill
USPC−1014
Harvard Forest
Gainesville Swale
Namekus Lake
USPC−1005
F
40
20
0
Pollen counts
0
500
1000
Number of individuals
interpolated
extrapolated
Dismal Swamp (VA)
USPC−1014
Camel Lake (FL)
Rockyhock Bay (NC)
USPC−1005
Cranberry Glades (Appalachia)

.

Fig. 4.3. Interpolation and Extrapolation rarefaction curves for fossil megaflora and palynoflora from Stenkul Fiord, Ellesmere Island. (A) Sample completeness (coverage) curve for megaflora samples from USPC-1005 and USPC-1014. Completeness value for each sample is > 95%, which suggests each collection was well-sampled. (B) Sample completeness (coverage) curves for palynoflora samples USPC-1005, USPC-1014, C-626937, and C-625852. Completeness value for each sample is > 95%, which suggests each collection was well-sampled. (C) Rarefaction curves for megaflora samples USPC-1005 and USPC-1014 which shows that the diversity of the two samples are similar, with minimal increase to standing diversity based on extrapolation estimates. (D) Rarefaction curves for palynoflora samples USPC-1005, USPC-1014, C-626937, and C-625852, which shows that the diversity of the four samples are similar, however, the coal samples (C-626937 & C-625852) appear to be less diverse than the mudstone samples. (E) Rarefaction curves of fossil megaflora samples USPC-1005 and USPC-1014 compared against modern day forests (see supplementary material), which demonstrates that the fossil sites have similar, although slightly lower, diversity to modern mid-latitude forests. (F) Rarefaction curves of fossil palynoflora samples USPC-1005 and USPC-1014 compared against modern day forests (see supplementary material), which demonstrates that the palynoflora has similar or higher diversity to palynofloras from modern mid-latitude forests.

5. CONCLUSIONS

The end result of this dissertation is a detailed assessment of the late Paleocene to early Eocene fossil flora from Ellesmere and Axel Heiberg islands that provides a perspective that is a synthesis of paleoecology, paleoclimatology, and systematics. Each facet provides a new layer of information and detail with which to reconstruct the ancient polar forests of northern Canada in the context of the greenhouse world of the early Eocene. Herein the major results of this study, and how they are interelated, are briefly summarized.

Paleobotanical evidence was presented (chapter 2) regarding the climate of Ellesmere Island during the late Paleocene and early Eocene. Estimates of temperature, precipitation and other climate variables were produced utilizing fossil flora from three localities on Ellesmere Island (i.e., Stenkul Fiord, Split Lake, and Strathcona Fiord). These fossils were organized into a preliminary morphotype framework, and using physiognomic methods (i.e., LAA, LMA, and CLAMP) climate estimates were produced. Climate was also reconstructed using the nearest living relative method Bioclimatic Analysis from existing pollen datasets from Stenkul Fiord on southern Ellesmere Island.

The temperature estimates agreed with previous proxy evidence, both isotopic and paleobotanical (Basinger et al., 1994; Greenwood and Wing, 1995; Jahren and Sternberg, 2003; Eberle et al., 2010; Greenwood et al., 2010). Growing season precipitation (GSP) estimates were produced using CLAMP, and although GSP estimates are typically unassignable to a specific season (i.e., winter, summer, spring, fall), in this case these GSP estimates could be assigned to the summer season, as this season would by necessity coincide with the summer light season of the high latitudes. Thus, the GSP estimates could be subtracted from the MAP estimates, produced from LAA, to produce rough estimates of winter-only precipitation. The summer and winter precipitation estimates were nearly equivocal (e.g., Stenkul Fiord median values of GSP ≈ 90 cm/yr, and WP ≈ 110 cm/yr), which contradicts prior isotopic evidence that reported a summer precipitation bias that was interpreted as a monsoonal climate signal (e.g., Eberle et al. 2012).

The precipitation data suggests that these high latitude environments were not only considerably wetter than previously thought, but also lacking in significant precipitation seasonality. Thus, the paleobotanical precipitation estimates agreed with climate models that showed the northern high latitudes as being 'ever-wet' or equable (e.g., Huber & Goldner, 2012). An 'ever-wet' or equable precipitation regime would necessitate a permanent to semi-permanent polar cloud cap, and may offer a partial explanation of how these high-latitude regions remained warm during prolonged periods of polar darkness. Photic seasonality, an intrinsic abiotic aspect of high latitude ecosystems, was suggested as a potential source for the Arctic 'summer bias', or monsoonal signal, observed in isotopic data recorded from fossil wood.

Building on the preliminary morphotypes established for climate analyses, additional morphotypes were established and described (chapter 3), and represent the first comprehensive taxonomic analysis of the late Paleocene–early Eocene Arctic Canada floras since the late 1800's (e.g., Heer 1878). Eighty-three plant megaflora morphotypes were established and described. A total of 65 morphotypes were identified as angiosperms (62 'dicots' and 3 monocotyledonous) morphotypes. An additional 13 morphotypes were identified as gymnosperms, and 5 morphotypes were recognized as pteridophytes.

The morphotypes represent 17 orders and 22 families; however, 31 morphotypes remain of unknown affinity, many of which comprise rarer, potentially unique, elements of the Canadian Arctic Flora. Families considered to be dominant elements within the Canadian Arctic Flora include: Cupressaceae, Cercidiphyllaceae, Betulaceae, Platanaceae, Fagaceae, Sapindaceae, and the Vitaceae. Rare elements, with assigned affinities, include the Magnoliaceae, Nelumbonaceae, Myricaceae, Juglandaceae, and the Rosaceae. The most common floral elements of the palaeoarctic forests from Northernmost Canada appear to be *Equisetum, Metasequoia, Glyptostrobus, Nyssidium, Trochodendroides, Ushia, Ulmus, Archeampelos, Aesculus, Quereuxia,* and *Vitiphyllum*.

These taxa have been recovered from most localities across both Ellesmere and Axel

Heiberg islands, and nearly all these taxa can be found at late Paleocene–early Eocene fossil localities elsewhere in the High Arctic. It should be noted that the commonness of these flora elements may represent either taphonomic or collectors bias, or both. Nevertheless, many of these taxa may also be found at contemporaneous fossil sites from the middle latitudes of North America, with some notable exceptions (e.g., *Ushia*). This would seem to suggest that the polar forests that occupied Ellesmere and Axel Heiberg islands were a circumpolar feature of the early Paleogene world (cf. Kvaček 2010), that mixed compositionally with mid-latitudes forests, a suggestion discussed by previous authors (e.g., Manchester 1999; Collinson & Hooker 2003).

Those morphotypes described from Ellesmere and Axel Heiberg islands that remain without assignment to formal taxa may eventually be identified to taxa from contemporaneous high or mid-latitude fossils sites. If this proves to be the case, these additional records would demonstrate a greater degree of uniformity between the high-latitude and mid-latitude forests. Nevertheless, these unidentified elements do suggest that some aspects of the polar forests in Canada were endemic to the region, an aspect not previously observed in existing palynofloras (Harrington 2004).

The monographic treatment of this flora necessitated that the history and concepts of the Arcto-Tertiary Geoflora, and the Polar Broadleaf Deciduous Forest, be explored. Prior evidence demonstrates that the idea of a ‘Geoflora’ is contradicted by the fossil record (Kvaček 2010; Grímsson et al., 2015); however, the similarity of this fossil flora to other contemporaneous fossil localities from both high- and mid-latitude localities from the late Paleocene and early Eocene does suggest that specific elements (e.g., *Metasequoia, Glyptostrobus, Nyssidium, Trochodendroides, Ushia*) persisted within these circumpolar forests for several million years, modified only by intermingling with mid-latitude forests encroaching northwards during hyperthermal intervals, and the inevitable cooling trend following the EECO towards the middle Eocene.

The presence of the Rosaceae (e.g., *Crataegus* and *Sorbaria*) family at high-latitudes, for example, suggests that these microthermal lineages (e.g. Wing, 1987; Pigg and DeVore, 2010) that had evolved in response to potentially cooler and drier microclimates in the mid-latitudes, a result of the newly formed uplands, of the early Eocene (e.g. Falkland, B.C; McAbee, B.C; and, Republic, WA) were able to exploit similar climatic conditions in the high Arctic.

Although the results from the monographic treatment suggest that these ecosystems supported a far more diverse flora than has been previously thought, early Eocene Arctic environments have been historically viewed as low diversity swamplands dominated by the Cupressaceae family (e.g. *Metasequoia*, *Glyptostrobus,* and *Taxodium*) with limited influence from broadleaf dicotyledonous angiosperms. This view of floral diversity in the Arctic has not been quantitatively tested using fossil megaflora, although one prior study examined floral diversity at Stenkul Fiord from fossil pollen (e.g., Harrington et al. 2012). In order to quantitatively test the vegetation diversity of the late Paleocene–early Eocene Arctic, fossil leaf collections were made, sampled census-style, from two well-constrained stratigraphic horizons at Stenkul Fiord on southern Ellesmere Island (chapter 4).

The two fossil collections were sampled from fossiliferous beds found within measured stratigraphic sections, that are constrained by U-Pb dating, and contain isotope signatures that record both the PETM and the ETM2. The fossil localities (USPC-1005 and USPC-1014) occur stratigraphically below the PETM, and stratigraphically above the ETM2, respectively. In addition, new pollen analyses were performed in order to compare floral diversity at both the local and regional scale. Pollen analyses was performed on sediment sourced from the same beds sampled for compression fossils, as well as stratigraphically nearby coal horizons in order counteract depositional system bias.

Floral diversity was evaluated primarily through rarefaction curves derived using census-count abundance data of the dicot compression fossils and the palynoflora. Sample completeness was assessed, for both census leaf data and pollen counts, which demonstrates that each fossil

locality was sufficiently well-sampled for diversity analysis. Traditional diversity metrics used in modern ecology (e.g. Simpson's Diversity, Shannon's Diversity Index, and Shannon's Evenness) were also calculated.

These data were compared against modern vegetation samples from the mid-latitudes of North America, which showed that the fossil flora from Stenkul Fiord had diversity similar to modern North American mid-latitude broadleaf deciduous forests. Furthermore, these analyses were able to demonstrate that the diversity, or species richness, of these forests remained relatively stable over time; however, the species composition of these forests did appear to change over time.

The cause for a change in floral composition between the two localities remains unresolved, although it is possible that these changes reflect depositional systems sampling different aspects of the forest at different times, or naturally occurring changes to a forest environment that might occur over long periods of time. Potentially these changes may have occurred in response to the hyperthermal events (i.e., PETM or ETM2) ongoing throughout the early Eocene.

Extratropical mid-latitude early Eocene sites considered hyper-diverse suggest that tropical-style diversity may have extended well into the mid-latitudes, a result of floral immigration due to the flattening of the latitudinal temperature gradient. This idea is supported by recent research evaluating diversity trends across latitudinal transects suggesting that temperature likely drove diversification in the tropics, with factors such as precipitation, insolation, and biological interaction constraining floral diversity in the extratropics.

Similar climate estimates have been reconstructed between mid-latitude upland and high-latitude lowland fossil localities, which suggests if temperature were the primary factor driving diversity in the extratropics then the reconstructed warm equable climate of the early Eocene Arctic suggest these high latitude forests should have been more diverse. Previous studies have suggested that photic seasonality in the high arctic may not have served as a significant obstacle to restricting biodiversity (Harrington et al. 2012). However, similar climatic context between

hyper-diverse mid-latitude fossil localities and high latitudes suggest that the seasonal photic regime and insolation may have been a constraining factor on floral diversity in the Arctic.

Extreme photic seasonality would have resulted in a significant form of stress for early Eocene Arctic vegetation, and as a result the extreme photic seasonality may have precluded additional floral taxa from exploiting high latitude regions. Indeed, those taxa capable of spreading into this non-analog environment may have been living at the edge of their ecological and climatic tolerance.

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Appendix A:

Supplemental Data for Chapter 2

GENERAL INFO | Morphotype Name: Split Lake 001 | Morphotype #: 029

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 442-2832.1

Localities & Specimens

442-2832.1

LEAF

Leaf Organization	simple	Base Angle	wide obtuse	Apex Angle	not visible
Laminar Size	microphyll	Base Shape	cordate		
CLAMP Size	microphyll 3	Apex Shape	not visible		
Laminar Shape	elliptic	Petiolar Attach.	marginal	Laminar L:W Ratio	1:1
Laminar Symmetry	symmetrical	Margin Type	serrate	Lobation	unlobed

1° to 3°

1° Vein Category	basal actinodromous	2° Vein Angle	uniform
2° Vein Category	interior	Inter-2° Veins	not visible
Agrophic Veins	simple	3° Vein Cat.	not visible
# of Basal Veins	5	3° Vein Course	not visible
2° Vein Spacing	uniform	3° Angle to 1°	not visible

PHOTO

TEETH

# of Orders	1
Teeth/cm	4
Spacing	regular
Shape	cv cv cv cc
Sinus	angular
Apex	simple

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Split Lake 002 | Morphotype #: 030

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 442-2810.1

Localities & Specimens

442-2810.1

LEAF

Leaf Organization	Simple	Base Angle	obtuse	Apex Angle	not visible
Laminar Size	notophyll	Base Shape	rounded		
CLAMP Size	mesophyll 1	Apex Shape	not visible		
Laminar Shape	not visible	Petiolar Attach.	marginal	Laminar L:W Ratio	n/a
Laminar Symmetry	not visible	Margin Type	erose	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	decreasing toward base
2° Vein Category	semicraspedodromous	Inter-2° Veins	not visible
Agrophic Veins	compound	3° Vein Cat.	not visible
# of Basal Veins	1	3° Vein Course	not visible
2° Vein Spacing	irregular	3° Angle to 1°	not visible

PHOTO

TEETH

# of Orders	n/a
Teeth/cm	
Spacing	
Shape	
Sinus	
Apex	

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Split Lake 003 | Morphotype #: 031

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 444-2748

Localities & Specimens

444-2748, -2840, -2841

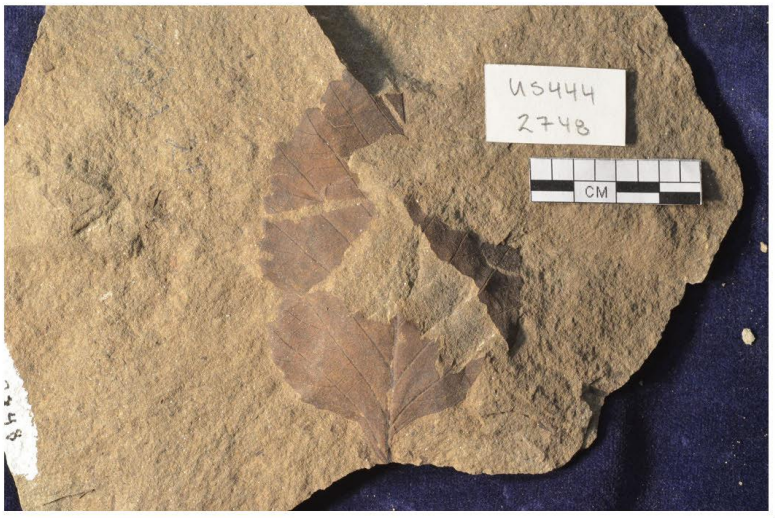
LEAF

Leaf Organization	simple	Base Angle	obtuse	Apex Angle	acute
Laminar Size	notophyll	Base Shape	concavo-convex		
CLAMP Size	mesophyll 1	Apex Shape	convex		
Laminar Shape	oblong / elliptic	Petiolar Attach.	marginal	Laminar L:W Ratio	2:1
Laminar Symmetry	base asymmetrical	Margin Type	crenate	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	smoothly decreasing toward base
2° Vein Category	craspedodromous	Inter-2° Veins	absent
Agrophic Veins	simple	3° Vein Cat.	mixed opp/alt
# of Basal Veins	1	3° Vein Course	straight
2° Vein Spacing	irregular	3° Angle to 1°	obtuse

PHOTO



TEETH

# of Orders	1				
Teeth/cm	3				
Spacing	regular				
Shape	cv	cv	cv	cv	
Sinus	rounded				
Apex	simple				

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Split Lake 004 | Morphotype #: 032

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 442-2820

Localities & Specimens

442-2820, -2813. 2814, 444-2842

LEAF

Leaf Organization	simple		Base Angle	wide obtuse	Apex Angle	acute	
Laminar Size	mesophyll		Base Shape	cordate			
CLAMP Size	mesophyll 2	mesophyll 3	Apex Shape	convex			
Laminar Shape	elliptic		Petiolar Attach.	marginal	Laminar L:W Ratio	1:1	
Laminar Symmetry	symmetrical		Margin Type	dentate	Lobation	unlobed	

1° to 3°

1° Vein Category	actinodromous	2° Vein Angle	regular
2° Vein Category	craspedodromous	Inter-2° Veins	absent
Agrophic Veins	compound	3° Vein Cat.	opposite percurrent
# of Basal Veins	5	3° Vein Course	convex
2° Vein Spacing	regular	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	1			
Teeth/cm	5			
Spacing	regular			
Shape	cv	st	cv	cc
Sinus	angular			
Apex	simple			

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO Morphotype Name: Split Lake 005 Morphotype #: 033

Major Plant Group: DIC Organ Type: Leaf Type Spec. #: 442-2811

Localities & Specimens

442-2811

LEAF

Leaf Organization	simple	Base Angle	wide obtuse	Apex Angle	not visible
Laminar Size	mesophyll	Base Shape	cordate		
CLAMP Size	mesophyll 3	Apex Shape	not visible		
Laminar Shape	elliptic	Petiolar Attach.	marginal	Laminar L:W Ratio	1:1
Laminar Symmetry	symmetrical	Margin Type	crenate	Lobation	palmately

1° to 3°

1° Vein Category	actinodromous	2° Vein Angle	uniform
2° Vein Category	craspedodromous	Inter-2° Veins	absent
Agrophic Veins	compound	3° Vein Cat.	mixed opp/alt
# of Basal Veins	6	3° Vein Course	straight
2° Vein Spacing	irregular	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	1				
Teeth/cm	4				
Spacing	regular				
Shape	cv	st	cv	cc	
Sinus	angular				
Apex	simple				

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Split Lake 006 | Morphotype #: 034

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 444-2838.2

Localities & Specimens

444-2838.1 (.2)

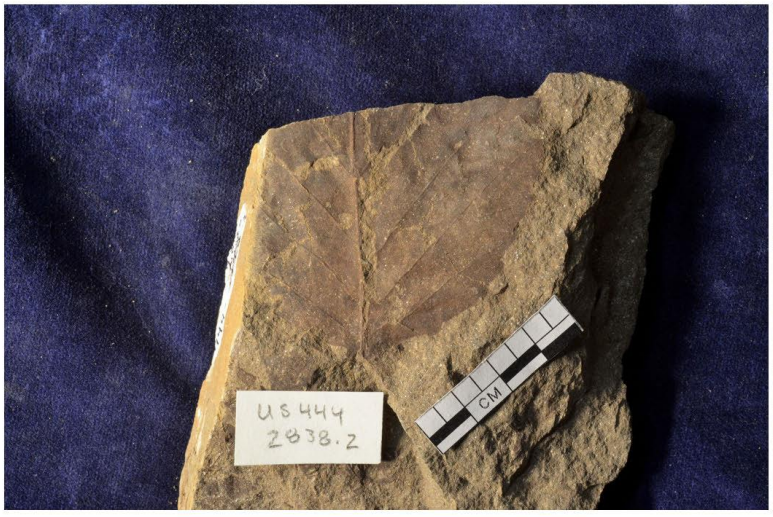
LEAF

Leaf Organization	simple	Base Angle	obtuse	Apex Angle	not visible
Laminar Size	notophyll	Base Shape	convex		
CLAMP Size	mesophyll 2	Apex Shape	not visible		
Laminar Shape	not visible	Petiolar Attach.	marginal	Laminar L:W Ratio	n/a
Laminar Symmetry	symmetrical	Margin Type	serrate	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	uniform
2° Vein Category	craspedodromous	Inter-2° Veins	absent
Agrophic Veins	simple	3° Vein Cat.	not visible
# of Basal Veins	1	3° Vein Course	not visible
2° Vein Spacing	uniform	3° Angle to 1°	not visible

PHOTO



TEETH

# of Orders	1
Teeth/cm	2
Spacing	regular
Shape	cv cc st cc
Sinus	rounded
Apex	simple

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO

Morphotype Name:	Split Lake 007		**Morphotype #:**	035	
Major Plant Group:	DIC	**Organ Type:**	Leaf	**Type Spec. #:**	442-2816

Localities & Specimens

442-2830, -2821. -2815, -2817, -2816

LEAF

Leaf Organization	simple		**Base Angle**	acute	**Apex Angle** acute
Laminar Size	microphyll		**Base Shape**	cuneate	
CLAMP Size	microphyll 3	mesophyll 1	**Apex Shape**	convex	
Laminar Shape	obovate		**Petiolar Attach.**	marginal	**Laminar L:W Ratio** 2:1
Laminar Symmetry	symmetrical		**Margin Type**	serrate/erose	**Lobation** unlobed

1° to 3°

1° Vein Category	pinnate	**2° Vein Angle**	uniform
2° Vein Category	craspedodromous	**Inter-2° Veins**	absent
Agrophic Veins	simple	**3° Vein Cat.**	not visible
# of Basal Veins	1	**3° Vein Course**	not visible
2° Vein Spacing	increasing toward base	**3° Angle to 1°**	not visible

PHOTO

TEETH

# of Orders	1
Teeth/cm	4
Spacing	regular
Shape	cv st cv cv
Sinus	angular
Apex	simple

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO Morphotype Name: Split Lake 008 | Morphotype #: 036

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 444-2839

Localities & Specimens

444-2839

LEAF

Leaf Organization	simple	Base Angle	obtuse	Apex Angle	acute
Laminar Size	notophyll	Base Shape	rounded		
CLAMP Size	mesophyll 1	Apex Shape	convex		
Laminar Shape	ovate	Petiolar Attach.	marginal	Laminar L:W Ratio	1.5:1
Laminar Symmetry	symmetrical	Margin Type	crenate	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	uniform
2° Vein Category	semicraspedodromous	Inter-2° Veins	absent
Agrophic Veins	not visible	3° Vein Cat.	opposite percurrent
# of Basal Veins	1	3° Vein Course	straight
2° Vein Spacing	irregular	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	1
Teeth/cm	3
Spacing	regular
Shape	cv cv
Sinus	rounded
Apex	simple

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Split Lake 009 | Morphotype #: 037

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 442-2818.2

Localities & Specimens

444-2818.1 (.2), -2813

LEAF

Leaf Organization	simple	Base Angle	wide obtuse	Apex Angle	not visible
Laminar Size	mesophyll	Base Shape	cordate		
CLAMP Size	mesophyll 3	Apex Shape	not visible		
Laminar Shape	elliptic	Petiolar Attach.	marginal	Laminar L:W Ratio	1.5:1
Laminar Symmetry	symmetrical	Margin Type	dentate/crenate	Lobation	unlobed

1° to 3°

1° Vein Category	actinodromous	2° Vein Angle	uniform
2° Vein Category	craspedodromous	Inter-2° Veins	absent
Agrophic Veins	compound	3° Vein Cat.	alternate percurrent
# of Basal Veins	5	3° Vein Course	convex
2° Vein Spacing	irregular	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	1			
Teeth/cm	3			
Spacing	regular			
Shape	cv	cv		
Sinus	angular			
Apex	simple			

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Split Lake 010 | Morphotype #: 038

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 444-2849

Localities & Specimens

444-2849

LEAF

Leaf Organization	simple	Base Angle	obtuse	Apex Angle	obtuse
Laminar Size	microphyll	Base Shape	concave		
CLAMP Size	microphyll 3	Apex Shape	complex		
Laminar Shape	elliptic	Petiolar Attach.	marginal	Laminar L:W Ratio	1:1
Laminar Symmetry	symmetrical	Margin Type	entire	Lobation	unlobed

1° to 3°

1° Vein Category	actinodromous	2° Vein Angle	not visible
2° Vein Category	not visible	Inter-2° Veins	not visible
Agrophic Veins	not visible	3° Vein Cat.	not visible
# of Basal Veins	not visible	3° Vein Course	not visible
2° Vein Spacing	not visible	3° Angle to 1°	not visible

PHOTO

TEETH

# of Orders	n/a
Teeth/cm	
Spacing	
Shape	
Sinus	
Apex	

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Split Lake 011 | Morphotype #: 039

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 444-2846

Localities & Specimens

444-2846

LEAF

Leaf Organization	simple	Base Angle	obtuse	Apex Angle	acute
Laminar Size	microphyll	Base Shape	concavo-convex		
CLAMP Size	microphyll 3	Apex Shape	acuminate		
Laminar Shape	elliptic	Petiolar Attach.	marginal	Laminar L:W Ratio	2:1
Laminar Symmetry	symmetrical	Margin Type	entire/erose	Lobation	unlobed

1° to 3°

1° Vein Category	actinodromous	2° Vein Angle	uniform
2° Vein Category	weakly brochidodromous	Inter-2° Veins	absent
Agrophic Veins	not visible	3° Vein Cat.	not visible
# of Basal Veins	5	3° Vein Course	not visible
2° Vein Spacing	uniform	3° Angle to 1°	not visible

PHOTO

TEETH

# of Orders	n/a
Teeth/cm	
Spacing	
Shape	
Sinus	
Apex	

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Stenkul Fiord 001 | Morphotype #: 001

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 438-2799

Localities & Specimens

438-2799, -2794

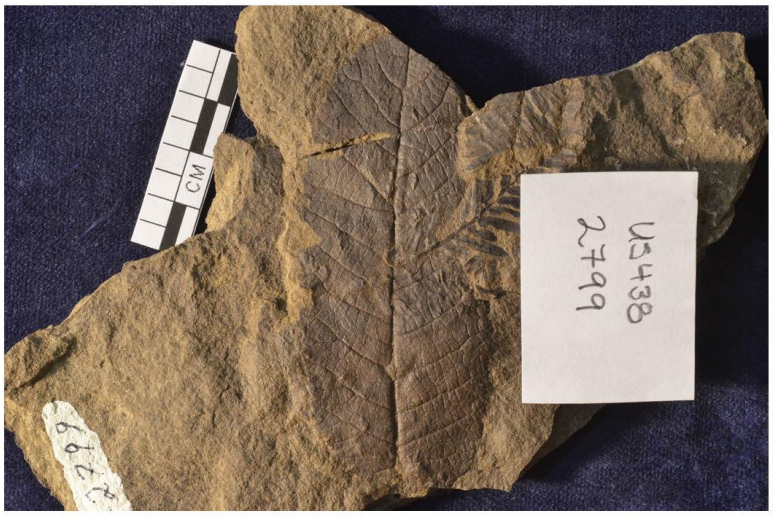
LEAF

Leaf Organization	Simple	Base Angle	acute	Apex Angle	not visible
Laminar Size	microphyll / notophyll	Base Shape	rounded		
CLAMP Size	microphyll 3 / mesophyll 1	Apex Shape	not visible		
Laminar Shape	elliptic	Petiolar Attach.	marginal	Laminar L:W Ratio	2:1
Laminar Symmetry	symmetrical	Margin Type	serrate	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	uniform
2° Vein Category	craspedodromous	Inter-2° Veins	absent
Agrophic Veins	absent	3° Vein Cat.	alternate percurrent
# of Basal Veins	1	3° Vein Course	not visible
2° Vein Spacing	irregular	3° Angle to 1°	not visible

PHOTO



TEETH

# of Orders	1
Teeth/cm	1.5
Spacing	regular
Shape	cc / cc
Sinus	angular
Apex	simple

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Stenkul Fiord 002 | Morphotype #: 002

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 436-2666.1

Localities & Specimens

436-2666.1

LEAF

Leaf Organization	Simple	Base Angle	not visible	Apex Angle	acute
Laminar Size	not visible	Base Shape	not visible		
CLAMP Size	not visible	Apex Shape	acuminate		
Laminar Shape	ovate	Petiolar Attach.	entire	Laminar L:W Ratio	n/a
Laminar Symmetry	symmetrical	Margin Type	entire	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	uniform
2° Vein Category	weakly brochidodromous	Inter-2° Veins	not visible
Agrophic Veins	not visible	3° Vein Cat.	not visible
# of Basal Veins	incomplete	3° Vein Course	not visible
2° Vein Spacing	increasing towards base	3° Angle to 1°	not visible

PHOTO

TEETH

# of Orders	n/a
Teeth/cm	
Spacing	
Shape	
Sinus	
Apex	

CUTICLE

Leaf Texture	
Stomata	
Features	

GENERAL INFO | Morphotype Name: Stenkul Fiord 003 | Morphotype #: 003

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 436-2753.2

Localities & Specimens

436-2753.2

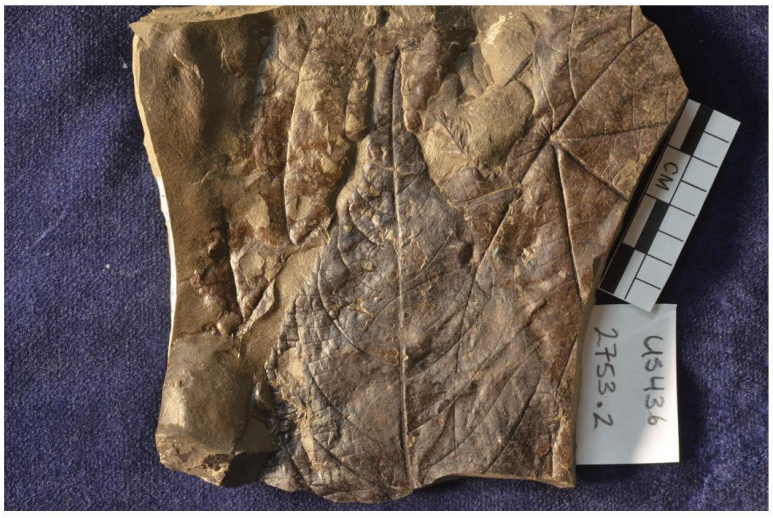
LEAF

Leaf Organization	Simple	Base Angle	not visible	Apex Angle	acute
Laminar Size	not visible	Base Shape	not visible		
CLAMP Size	not visible	Apex Shape	acuminate		
Laminar Shape	not visible	Petiolar Attach.	not visible	Laminar L:W Ratio	n/a
Laminar Symmetry	not visible	Margin Type	serrate	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	smoothly decreasing
2° Vein Category	semicraspedodromous	Inter-2° Veins	weak
Agrophic Veins	not visible	3° Vein Cat.	not visible
# of Basal Veins	not visible	3° Vein Course	not visible
2° Vein Spacing	increasing toward base	3° Angle to 1°	not visible

PHOTO



TEETH

# of Orders	1				
Teeth/cm	4				
Spacing	regular				
Shape	cv	cv			
Sinus	angular				
Apex	simple				

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Stenkul Fiord 004 | Morphotype #: 004

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 436-2751

Localities & Specimens

436-2751, -2736.1 (.2), -2757, -2764

LEAF

Leaf Organization	simple		Base Angle	wide obtuse	Apex Angle	acute
Laminar Size	microphyll	notophyll	Base Shape	cordate		
CLAMP Size	microphyll 3	mesophyll 1	Apex Shape	convex		
Laminar Shape	elliptic		Petiolar Attach.	marginal	Laminar L:W Ratio	1:1
Laminar Symmetry	symmetrical		Margin Type	dentate	Lobation	palmately

1° to 3°

1° Vein Category	palinactinodromous	2° Vein Angle	uniform
2° Vein Category	craspedodromous	Inter-2° Veins	weak
Agrophic Veins	simple	3° Vein Cat.	alternate percurrent
# of Basal Veins	5	3° Vein Course	straight
2° Vein Spacing	irregular	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	2			
Teeth/cm	3			
Spacing	irregular			
Shape	cv	cv		
Sinus	rounded			
Apex	simple			

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Stenkul Fiord 005 | Morphotype #: 005

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 436-2769.1

Localities & Specimens

436-2769.1 (.2), -2141.1 (.2), -2739, -2756.1

LEAF

Leaf Organization	Simple		Base Angle	obtuse	Apex Angle	obtuse
Laminar Size	notophyll	mesophyll	Base Shape	rounded		
CLAMP Size	mesophyll 2		Apex Shape	rounded		
Laminar Shape	obovate		Petiolar Attach.	marginal	Laminar L:W Ratio	~ 1.5:1
Laminar Symmetry	symmetrical		Margin Type	dentate	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	uniform
2° Vein Category	craspedodromous	Inter-2° Veins	absent
Agrophic Veins	simple	3° Vein Cat.	opposite percurrent
# of Basal Veins	4	3° Vein Course	convex
2° Vein Spacing	increasing toward base	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	1				
Teeth/cm	7				
Spacing	regular				
Shape	cv	cc	cv	cv	
Sinus	angular				
Apex	simple				

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Stenkul Fiord 006 | Morphotype #: 006

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 436-2730

Localities & Specimens

436-2730, -2734.2, -2667

LEAF

Leaf Organization	Simple	Base Angle	wide obtuse	Apex Angle	obtuse
Laminar Size	mesophyll	Base Shape	cordate		
CLAMP Size	mesophyll 3	Apex Shape	convex		
Laminar Shape	elliptic	Petiolar Attach.	marginal	Laminar L:W Ratio	2:1
Laminar Symmetry	symmetrical	Margin Type	dentate/erose	Lobation	palmately

1° to 3°

1° Vein Category	palinactinodromous	2° Vein Angle	uniform
2° Vein Category	craspedodromous	Inter-2° Veins	absent
Agrophic Veins	simple	3° Vein Cat.	alternate percurrent
# of Basal Veins	5	3° Vein Course	convex
2° Vein Spacing	increasing toward base	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	1			
Teeth/cm	6			
Spacing	regular			
Shape	cv	cv	cv	st
Sinus	angular			
Apex	simple			

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO	Morphotype Name:	Stenkul Fiord 007	Morphotype #:	007
Major Plant Group:	DIC	Organ Type:	Leaf	Type Spec. #:	439-2692

Localities & Specimens

439-2692, -2694 (A'-A"), 438-2785

LEAF

Leaf Organization	Simple		Base Angle	not visible	Apex Angle	acute
Laminar Size	microphyll	notophyll	Base Shape	not visible		
CLAMP Size	microphyll 2	microphyll 3	Apex Shape	convex		
Laminar Shape	ovate		Petiolar Attach.	not visible	Laminar L:W Ratio	2:1
Laminar Symmetry	symmetrical		Margin Type	serrate	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	uniform
2° Vein Category	craspedodromous	Inter-2° Veins	absent
Agrophic Veins	not visible	3° Vein Cat.	alternate percurrent
# of Basal Veins	not visible	3° Vein Course	straight
2° Vein Spacing	decreasing toward base	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	2
Teeth/cm	3
Spacing	regular
Shape	cv cv
Sinus	angular
Apex	simple

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | **Morphotype Name:** Stenkul Fiord 008 | **Morphotype #:** 008

Major Plant Group: DIC | **Organ Type:** Leaf | **Type Spec. #:** 435-2723

Localities & Specimens

435-2723, -2722, 439-2686.1 (.2), -2806, -2687

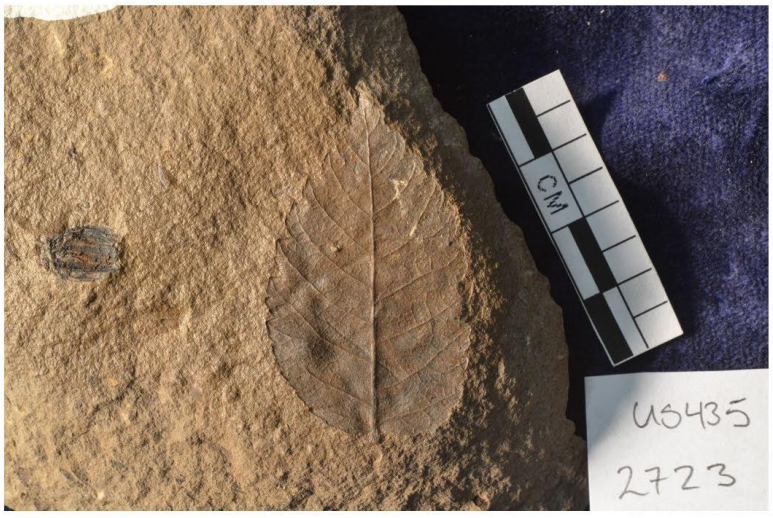
LEAF

Leaf Organization	Simple		**Base Angle**	obtuse	**Apex Angle**	acute
Laminar Size	microphyll	notophyll	**Base Shape**	rounded		
CLAMP Size	microphyll 2	microphyll 3	**Apex Shape**	convex		
Laminar Shape	ovate		**Petiolar Attach.**	marginal	**Laminar L:W Ratio**	2:1
Laminar Symmetry	symmetrical		**Margin Type**	serrate	**Lobation**	unlobed

1° to 3°

1° Vein Category	pinnate	**2° Vein Angle**	uniform
2° Vein Category	craspedodromous	**Inter-2° Veins**	absent
Agrophic Veins	simple	**3° Vein Cat.**	opposite percurrent
# of Basal Veins	4	**3° Vein Course**	convex
2° Vein Spacing	irregular	**3° Angle to 1°**	obtuse

PHOTO



TEETH

# of Orders	2
Teeth/cm	6
Spacing	regular
Shape	cv st cv cv
Sinus	angular
Apex	simple

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Stenkul Fiord 009 | Morphotype #: 009

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 438-2790

Localities & Specimens

439-2687 A''', -2804, -2689 A', 438-2790, -2783.1 (.2)

LEAF

Leaf Organization	Simple	Base Angle	not visible	Apex Angle	acute
Laminar Size	microphyll	Base Shape	not visible		
CLAMP Size	microphyll 1 / microphyll 2	Apex Shape	convex		
Laminar Shape	ovate	Petiolar Attach.	marginal	Laminar L:W Ratio	2:1
Laminar Symmetry	symmetrical	Margin Type	serrate	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	uniform
2° Vein Category	craspedodromous	Inter-2° Veins	weak
Agrophic Veins	not visible	3° Vein Cat.	mixed opp/alt
# of Basal Veins	not visible	3° Vein Course	straight
2° Vein Spacing	increasing toward base	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	1
Teeth/cm	3
Spacing	regular
Shape	cv / cv
Sinus	angular
Apex	simple

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Stenkul Fiord 010 | Morphotype #: 010

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 435-2706.1

Localities & Specimens

435-2706.1 (.2), 436-2743

LEAF

Leaf Organization	Simple	Base Angle	wide obtuse	Apex Angle	obtuse
Laminar Size	notophyll	Base Shape	cordate		
CLAMP Size	mesophyll 1	Apex Shape	rounded		
Laminar Shape	elliptic	Petiolar Attach.	marginal	Laminar L:W Ratio	1:1
Laminar Symmetry	symmetrical	Margin Type	dentate	Lobation	unlobed

1° to 3°

1° Vein Category	basal actinodromous	2° Vein Angle	smooth decrease toward base
2° Vein Category	semicraspedodromous	Inter-2° Veins	absent
Agrophic Veins	compound	3° Vein Cat.	opposite percurrent
# of Basal Veins	5	3° Vein Course	straight
2° Vein Spacing	increasing toward base	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	1			
Teeth/cm	5			
Spacing	regular			
Shape	cv	cv	st	cc
Sinus	rounded			
Apex	simple			

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Stenkul Fiord 011 | Morphotype #: 011

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 436-2747.1

Localities & Specimens

436-2747.1, -2749.1, 438-2795, 435-2712, 433-2675, -2676

LEAF

Leaf Organization	Simple	Base Angle	obtuse	Apex Angle	obtuse
Laminar Size	notophyll	Base Shape	truncate		
CLAMP Size	mesophyll 1	Apex Shape	convex		
Laminar Shape	ovate	Petiolar Attach.	marginal	Laminar L:W Ratio	1:1
Laminar Symmetry	symmetrical	Margin Type	crenate/erose	Lobation	unlobed

1° to 3°

1° Vein Category	basal actinodromous	2° Vein Angle	uniform
2° Vein Category	craspedodromous	Inter-2° Veins	weak
Agrophic Veins	simple	3° Vein Cat.	not visible
# of Basal Veins	5	3° Vein Course	not visible
2° Vein Spacing	increasing toward base	3° Angle to 1°	not visible

PHOTO

TEETH

# of Orders	1
Teeth/cm	5
Spacing	regular
Shape	cv cv
Sinus	rounded
Apex	simple

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Stenkul Fiord 012 | Morphotype #: 012 | Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 438-2796.1

Localities & Specimens

438-2796.1 (.2)

LEAF

Leaf Organization	Simple	Base Angle	not visible	Apex Angle	acute
Laminar Size	notophyll	Base Shape	not visible		
CLAMP Size	mesophyll 1	Apex Shape	convex		
Laminar Shape	not visible	Petiolar Attach.	not visible	Laminar L:W Ratio	n/a
Laminar Symmetry	not visible	Margin Type	entire/erose	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	uniform
2° Vein Category	craspedodromous	Inter-2° Veins	absent
Agrophic Veins	not visible	3° Vein Cat.	not visible
# of Basal Veins	not visible	3° Vein Course	not visible
2° Vein Spacing	increasing toward base	3° Angle to 1°	not visible

PHOTO

TEETH

# of Orders	n/a
Teeth/cm	
Spacing	
Shape	
Sinus	
Apex	

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | **Morphotype Name:** Stenkul Fiord 013 | **Morphotype #:** 013

Major Plant Group: DIC | **Organ Type:** Leaf | **Type Spec. #:** 436-2752.1

Localities & Specimens

436.2752.1 (.2)

LEAF

Leaf Organization	Simple	**Base Angle**	obtuse	**Apex Angle**	not visible
Laminar Size	mesophyll	**Base Shape**	rounded		
CLAMP Size	mesophyll 3	**Apex Shape**	not visible		
Laminar Shape	obovate	**Petiolar Attach.**	marginal	**Laminar L:W Ratio**	~ 2:1
Laminar Symmetry	base asymmetrical	**Margin Type**	serrate	**Lobation**	unlobed

1° to 3°

1° Vein Category	suprabasal acrodromous	**2° Vein Angle**	irregular
2° Vein Category	interior	**Inter-2° Veins**	weak
Agrophic Veins	simple	**3° Vein Cat.**	opposite percurrent
# of Basal Veins	8	**3° Vein Course**	straight
2° Vein Spacing	irregular	**3° Angle to 1°**	obtuse

PHOTO

TEETH

# of Orders	1
Teeth/cm	5
Spacing	regular
Shape	st / fl / cv / cc
Sinus	angular
Apex	simple

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Stenkul Fiord 014 | Morphotype #: 014 | Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 439-2801.1

Localities & Specimens

439-2801.1 (.2)

LEAF

Leaf Organization	Simple	Base Angle	wide obtuse	Apex Angle	not visible
Laminar Size	mesophyll	Base Shape	cordate		
CLAMP Size	mesophyll 3	Apex Shape	not visible		
Laminar Shape	obovate	Petiolar Attach.	matginal	Laminar L:W Ratio	1:1
Laminar Symmetry	symmetrical	Margin Type	serrate	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	increasing toward base
2° Vein Category	craspedodromous	Inter-2° Veins	not visible
Agrophic Veins	simple	3° Vein Cat.	opposite percurrent
# of Basal Veins	not visible	3° Vein Course	straight
2° Vein Spacing	uniform	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	1
Teeth/cm	2
Spacing	regular
Shape	cv cc
Sinus	rounded/angular
Apex	simple

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | **Morphotype Name:** Stenkul Fiord 015 | **Morphotype #:** 015

Major Plant Group: DIC | **Organ Type:** Leaf | **Type Spec. #:** 435-2714

Localities & Specimens

435-2714, -2701, 2710.2

LEAF

Leaf Organization	Simple	**Base Angle**	not visible	**Apex Angle**	acute
Laminar Size	notophyll	**Base Shape**	not visible		
CLAMP Size	mesophyll 1	**Apex Shape**	convex		
Laminar Shape	ovate	**Petiolar Attach.**	marginal	**Laminar L:W Ratio**	2:1
Laminar Symmetry	symmetrical	**Margin Type**	crenate	**Lobation**	

1° to 3°

1° Vein Category	pinnate	**2° Vein Angle**	regular
2° Vein Category	craspedodromous	**Inter-2° Veins**	absent
Agrophic Veins	simple	**3° Vein Cat.**	opposite percurrent
# of Basal Veins	1	**3° Vein Course**	straight
2° Vein Spacing	increasing toward base	**3° Angle to 1°**	obtuse

PHOTO

TEETH

# of Orders	1
Teeth/cm	3
Spacing	regular
Shape	rt / cv / cv / cv
Sinus	rounded
Apex	simple

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Stenkul Fiord 016 | Morphotype #: 016

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 436-2663

Localities & Specimens

436-2663

LEAF

Leaf Organization	simple	Base Angle	acute	Apex Angle	acute
Laminar Size	mesophyll	Base Shape	convex		
CLAMP Size	mesophyll 3	Apex Shape	acuminate		
Laminar Shape	elliptic	Petiolar Attach.	marginal	Laminar L:W Ratio	2:1
Laminar Symmetry	base asymmetrical	Margin Type	serrate	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	uniform
2° Vein Category	craspedodromous	Inter-2° Veins	absent
Agrophic Veins	simple	3° Vein Cat.	opposite percurrent
# of Basal Veins	4	3° Vein Course	convex
2° Vein Spacing	uniform	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	1
Teeth/cm	3
Spacing	regular
Shape	cv cc
Sinus	angular/rounded
Apex	simple

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Stenkul Fiord 017 | Morphotype #: 018 | Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 436-xxxx

Localities & Specimens

436-xxxx, -2749, 439-2807.1 (.2, .3)

LEAF

Leaf Organization	simple	Base Angle	acute	Apex Angle	not visible
Laminar Size	mesophyll	Base Shape	decurrent		
CLAMP Size	mesophyll 3	Apex Shape	not visible		
Laminar Shape	obovate	Petiolar Attach.	marginal	Laminar L:W Ratio	2:1
Laminar Symmetry	symmetrical	Margin Type	entire	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	uniform
2° Vein Category	weak brochidodromous	Inter-2° Veins	absent
Agrophic Veins	absent	3° Vein Cat.	mixed opp/alt
# of Basal Veins	1	3° Vein Course	straight
2° Vein Spacing	uniform	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	n/a
Teeth/cm	
Spacing	
Shape	
Sinus	
Apex	

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Stenkul Fiord 018 | Morphotype #: 019 | Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 438-2793

Localities & Specimens

438-2793

LEAF

Leaf Organization	Simple	Base Angle	not visible	Apex Angle	not visible
Laminar Size	mesophyll	Base Shape	not visible		
CLAMP Size	mesophyll 3	Apex Shape	not visible		
Laminar Shape	elliptic	Petiolar Attach.	not visible	Laminar L:W Ratio	n/a
Laminar Symmetry	not visible	Margin Type	dentate/crenate	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	uniform
2° Vein Category	semicraspedodromous	Inter-2° Veins	weak
Agrophic Veins	not visible	3° Vein Cat.	mixed opp/alt
# of Basal Veins	1	3° Vein Course	straight
2° Vein Spacing	irregular	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	1	
Teeth/cm	3	
Spacing	irregular	
Shape	cv	cv
Sinus	rounded	
Apex	simple	

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Stenkul Fiord 019 | Morphotype #: 020

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 435.2718.2

Localities & Specimens

435-2718.2, -2719.1, -2720.1

LEAF

Leaf Organization	Simple		Base Angle	acute	Apex Angle: not visible
Laminar Size	notophyll	mesophyll	Base Shape	concave	
CLAMP Size	mesophyll 2	mesophyll 3	Apex Shape	not visible	
Laminar Shape	elliptic		Petiolar Attach.	marginal	Laminar L:W Ratio: 2:1
Laminar Symmetry	base asymmetrical		Margin Type	crenate	Lobation: unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	uniform
2° Vein Category	craspedodronous	Inter-2° Veins	absent
Agrophic Veins	compound	3° Vein Cat.	opposite percurrent
# of Basal Veins	1	3° Vein Course	straight
2° Vein Spacing	increasing toward base	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	1
Teeth/cm	2
Spacing	regular
Shape	rt / cv
Sinus	rounded
Apex	simple

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Stenkul Fiord 020 | Morphotype #: 021

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 435-2708.1

Localities & Specimens

435-2708.1

LEAF

Leaf Organization	simple	Base Angle	not visible	Apex Angle	acute
Laminar Size	not visible	Base Shape	not visible		
CLAMP Size	not visible	Apex Shape	straight		
Laminar Shape	not visible	Petiolar Attach.	not visible	Laminar L:W Ratio	n/a
Laminar Symmetry	not visible	Margin Type	serrate	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	uniform
2° Vein Category	craspedodromous	Inter-2° Veins	absent
Agrophic Veins	not visible	3° Vein Cat.	mixed opp/alt
# of Basal Veins	not visible	3° Vein Course	convex
2° Vein Spacing	smooth increase > base	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	1
Teeth/cm	4
Spacing	regular
Shape	cv / cc / rt / cv
Sinus	angular
Apex	simple

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO Morphotype Name: Stenkul Fiord 021 | Morphotype #: 024

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 438-2791

Localities & Specimens

438-2791

LEAF

Leaf Organization	Simple	Base Angle	obtuse	Apex Angle	acute
Laminar Size	notophyll	Base Shape	rounded		
CLAMP Size	mesophyll 2	Apex Shape	convex		
Laminar Shape	elliptic	Petiolar Attach.	marginal	Laminar L:W Ratio	~1:1
Laminar Symmetry	symmetrical	Margin Type	entire	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	uniform
2° Vein Category	eucamptodromous	Inter-2° Veins	absent
Agrophic Veins	not visible	3° Vein Cat.	not visible
# of Basal Veins	1	3° Vein Course	not visible
2° Vein Spacing	decreasing toward base	3° Angle to 1°	not visible

PHOTO

TEETH

# of Orders	n/a
Teeth/cm	
Spacing	
Shape	
Sinus	
Apex	

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Stenkul Fiord 022 | Morphotype #: 026

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 436-2735.1

Localities & Specimens

436-2735.1 (.2)

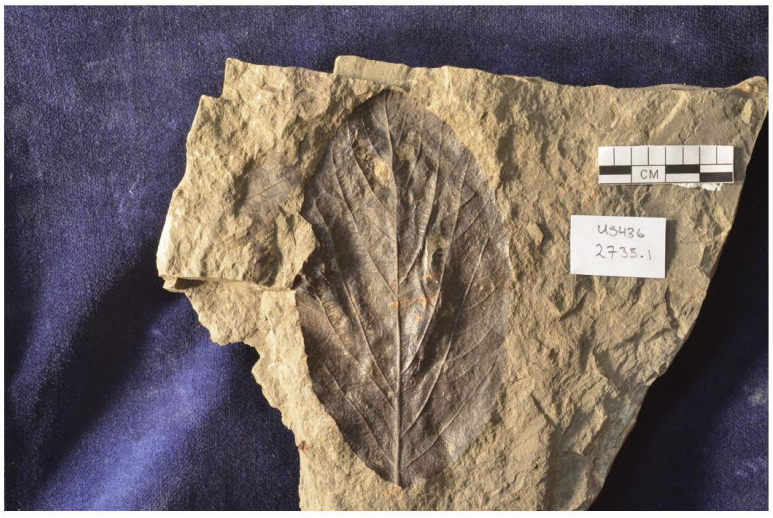
LEAF

Leaf Organization	simple	Base Angle	acute	Apex Angle	acute
Laminar Size	mesophyll	Base Shape	rounded		
CLAMP Size	mesophyll 2	Apex Shape	convex		
Laminar Shape	oblong	Petiolar Attach.	marginal	Laminar L:W Ratio	2:1
Laminar Symmetry	symmetrical	Margin Type	serrate	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	uniform
2° Vein Category	craspedodromous	Inter-2° Veins	absent
Agrophic Veins	simple	3° Vein Cat.	opposite percurrent
# of Basal Veins	5	3° Vein Course	straight
2° Vein Spacing	irregular	3° Angle to 1°	obtuse

PHOTO



TEETH

# of Orders	1
Teeth/cm	8
Spacing	regular
Shape	st cv
Sinus	rounded
Apex	simple

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Stenkul Fiord 023 | Morphotype #: 027

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 436-2732.2

Localities & Specimens

436-2732.1 (.2), -2729.1, -2681, -2666.1, -2759, 435-2605, -2698, 432-2669

LEAF

Leaf Organization	simple		Base Angle	wide obtuse	Apex Angle	acute
Laminar Size	notophyll	mesophyll	Base Shape	cordate		
CLAMP Size	mesophyll 1	mesophyll 2	Apex Shape	convex		
Laminar Shape	elliptic		Petiolar Attach.	marginal	Laminar L:W Ratio	~1:1
Laminar Symmetry	symmetrical		Margin Type	crenate	Lobation	palmately

1° to 3°

1° Vein Category	actinodromous	2° Vein Angle	uniform
2° Vein Category	craspedodromous	Inter-2° Veins	strong
Agrophic Veins	simple	3° Vein Cat.	alternate percurrent
# of Basal Veins	6	3° Vein Course	convex
2° Vein Spacing	increase toward base	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	1				
Teeth/cm	1				
Spacing	regular				
Shape	cv	cv			
Sinus	rounded				
Apex	simple				

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO	Morphotype Name:	Stenkul Fiord 024	Morphotype #:	055
Major Plant Group:	DIC	Organ Type:	Leaf	Type Spec. #:	439-2809.2

Localities & Specimens

439-2809.1 (.2)

LEAF

Leaf Organization	simple	Base Angle	wide obtuse	Apex Angle	acute
Laminar Size	notophyll	Base Shape	cordate		
CLAMP Size	microphyll 3	Apex Shape	convex		acuminate
Laminar Shape	ovate	Petiolar Attach.	marginal	Laminar L:W Ratio	1.5:1
Laminar Symmetry	symmetrical	Margin Type	erose	Lobation	unlobed

1° to 3°

1° Vein Category	actinodromous	2° Vein Angle	uniform
2° Vein Category	weakly brochidodromous	Inter-2° Veins	absent
Agrophic Veins	simple	3° Vein Cat.	not visible
# of Basal Veins	5	3° Vein Course	not visible
2° Vein Spacing	uniform	3° Angle to 1°	not visible

PHOTO

TEETH

# of Orders	n/a
Teeth/cm	
Spacing	
Shape	
Sinus	
Apex	

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Stenkul Fiord 025 | Morphotype #: 056

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 436-2750

Localities & Specimens

436-2750, -2744

LEAF

Leaf Organization	simple		Base Angle	wide obtuse	Apex Angle	acute
Laminar Size	microphyll	notophyll	Base Shape	cordate		
CLAMP Size	microphyll 2	microphyll 3	Apex Shape	acuminate		
Laminar Shape	elliptic		Petiolar Attach.	marginal	Laminar L:W Ratio	1:1
Laminar Symmetry	symmetrical		Margin Type	serrate	Lobation	unlobed

1° to 3°

1° Vein Category	actinodromous	2° Vein Angle	uniform
2° Vein Category	semicraspedodromous	Inter-2° Veins	absent
Agrophic Veins	simple	3° Vein Cat.	not visible
# of Basal Veins	6	3° Vein Course	not visible
2° Vein Spacing	uniform	3° Angle to 1°	not visible

PHOTO

TEETH

# of Orders	1			
Teeth/cm	4			
Spacing	irregular			
Shape	cv	st	cv	cc
Sinus	rounded			
Apex	simple			

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Strathcona Fiord 001 | Morphotype #: 040

Major Plant Group: DIC | Organ Type: Lake | Type Spec. #: 422-3869"

Localities & Specimens

422-3869",-3869,-3876

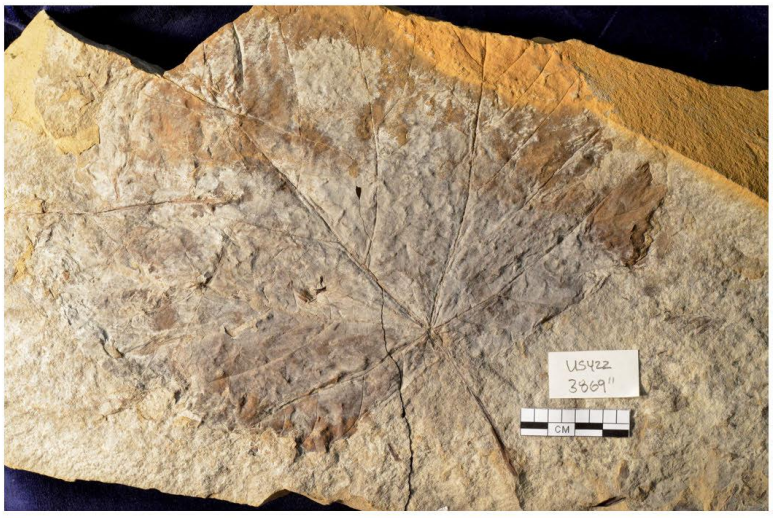
LEAF

Leaf Organization	simple	Base Angle	wide obtuse	Apex Angle	acute
Laminar Size	mesophyll	Base Shape	cordate		
CLAMP Size	microphyll 3	Apex Shape	convex		
Laminar Shape	elliptic	Petiolar Attach.	marginal	Laminar L:W Ratio	
Laminar Symmetry	symmetrical	Margin Type	dentate	Lobation	

1° to 3°

1° Vein Category	palinactinodromous	2° Vein Angle	uniform
2° Vein Category	interior	Inter-2° Veins	absent
Agrophic Veins	compound	3° Vein Cat.	not visible
# of Basal Veins	5	3° Vein Course	not visible
2° Vein Spacing	uniform	3° Angle to 1°	not visible

PHOTO



TEETH

# of Orders	1
Teeth/cm	2
Spacing	irregular
Shape	cv cv cv st
Sinus	angular/rounded
Apex	simple

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO Morphotype Name: Strathcona Fiord 002 | Morphotype #: 041

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 422-3874

Localities & Specimens

422-3874

LEAF

Leaf Organization	simple	Base Angle	acute	Apex Angle	acute
Laminar Size	mesophyll	Base Shape	cuneate		
CLAMP Size	mesophyll 3	Apex Shape	convex		
Laminar Shape	elliptic	Petiolar Attach.	marginal	Laminar L:W Ratio	3:1
Laminar Symmetry	symmetrical	Margin Type	erose	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	smoothly decreasing toward base
2° Vein Category	weak brochidromous	Inter-2° Veins	absent
Agrophic Veins	absent	3° Vein Cat.	mixed opp/alt
# of Basal Veins	1	3° Vein Course	straight
2° Vein Spacing	uniform	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	n/a
Teeth/cm	
Spacing	
Shape	
Sinus	
Apex	

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Strathcona Fiord 003 | Morphotype #: 042

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 422-3867

Localities & Specimens

422-3867, -3868, -3884

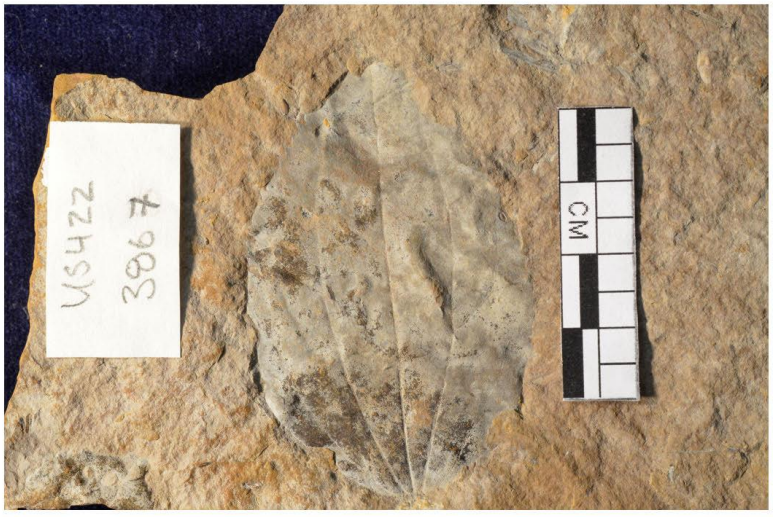
LEAF

Leaf Organization	simple	Base Angle	obtuse	Apex Angle	acute
Laminar Size	microphyll	Base Shape	rounded		
CLAMP Size	microphyll 3	Apex Shape	convex		
Laminar Shape	elliptic / ovate	Petiolar Attach.	marginal	Laminar L:W Ratio	2:1
Laminar Symmetry	symmetrical	Margin Type	serrate	Lobation	unlobed

1° to 3°

1° Vein Category	basal acrodromous	2° Vein Angle	uniform
2° Vein Category	acrodromous	Inter-2° Veins	absent
Agrophic Veins	absent	3° Vein Cat.	not visible
# of Basal Veins	5	3° Vein Course	not visible
2° Vein Spacing	uniform	3° Angle to 1°	not visible

PHOTO



TEETH

# of Orders	1
Teeth/cm	3.5
Spacing	regular
Shape	cv / st / st / cc
Sinus	angular
Apex	simple

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Strathcona Fiord 004 | Morphotype #: 043

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 422-3871

Localities & Specimens

422-3871, -3881. -3874 (lower)

LEAF

Leaf Organization	simple	Base Angle	wide obtuse	Apex Angle	acute
Laminar Size	mesophyll	Base Shape	cordate		
CLAMP Size	mesophyll 2	Apex Shape	acuminate		
Laminar Shape	elliptic	Petiolar Attach.	marginal	Laminar L:W Ratio	1.5:1
Laminar Symmetry	symmetrical	Margin Type	serrate	Lobation	unlobed

1° to 3°

1° Vein Category	basal actinodromous	2° Vein Angle	uniform
2° Vein Category	craspedodromous	Inter-2° Veins	absent
Agrophic Veins	compound	3° Vein Cat.	not visible
# of Basal Veins	9	3° Vein Course	not visible
2° Vein Spacing	uniform	3° Angle to 1°	not visible

PHOTO

TEETH

# of Orders	1
Teeth/cm	3
Spacing	irregular
Shape	cv st cv rt
Sinus	angular
Apex	simple

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Strathcona Fiord 005 | Morphotype #: 044

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 422-3883

Localities & Specimens

422-3883, -3806', -3873

LEAF

Leaf Organization	simple	Base Angle	not visible	Apex Angle	acute
Laminar Size	mesophyll	Base Shape	not visible		
CLAMP Size	mesophyll 1	Apex Shape	acuminate		
Laminar Shape	ovate	Petiolar Attach.	not visible	Laminar L:W Ratio	1.5:1
Laminar Symmetry	symmetrical	Margin Type	serrate/erose	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	uniform
2° Vein Category	weak brochidromous	Inter-2° Veins	absent
Agrophic Veins	not visible	3° Vein Cat.	mixed opp/alt
# of Basal Veins	not visible	3° Vein Course	convex/sinous
2° Vein Spacing	uniform	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	1			
Teeth/cm	4			
Spacing	irregular			
Shape	cv	st	cv	cc
Sinus	rounded			
Apex	simple			

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Strathcona Fiord 006 | Morphotype #: 045

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 422-3876 (reverse)

Localities & Specimens

422-3876 (reverse)

LEAF

Leaf Organization	simple	Base Angle	not visible	Apex Angle	acute
Laminar Size	mesophyll	Base Shape	not visible		
CLAMP Size	mesophyll 3	Apex Shape	acuminate		
Laminar Shape	elliptic	Petiolar Attach.	not visible	Laminar L:W Ratio	
Laminar Symmetry	not visible	Margin Type	serrate/erose	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	uniform
2° Vein Category	craspedodromous	Inter-2° Veins	weak
Agrophic Veins	not visible	3° Vein Cat.	alternate percurrent
# of Basal Veins	not visible	3° Vein Course	convev
2° Vein Spacing	uniform	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	1			
Teeth/cm	3			
Spacing	regular			
Shape	cv	cv	cv	st
Sinus	angular			
Apex	simple			

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Strathcona Fiord 007 | Morphotype #: 046

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 422-3879'L

Localities & Specimens

422-3879, -3879'L

LEAF

Leaf Organization	simple	Base Angle	not visible	Apex Angle	acute
Laminar Size	microphyll	Base Shape	not visible		
CLAMP Size	microphyll 2	Apex Shape	convex		
Laminar Shape	ovate	Petiolar Attach.	not visible	Laminar L:W Ratio	2:1
Laminar Symmetry	not visible	Margin Type	serrate	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	uniform
2° Vein Category	semicraspedodromous	Inter-2° Veins	absent
Agrophic Veins	absent	3° Vein Cat.	mixed opp/alt
# of Basal Veins	not visible	3° Vein Course	straight
2° Vein Spacing	irregular	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	1
Teeth/cm	6
Spacing	regular
Shape	cv st
Sinus	angular
Apex	simple

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Strathcona Fiord 008 | Morphotype #: 047

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 422-3879'

Localities & Specimens

422-3879', -3880

LEAF

Leaf Organization	simple	Base Angle	obtuse	Apex Angle	acute
Laminar Size	notophyll	Base Shape	rounded		
CLAMP Size	microphyll 3	Apex Shape	convex		
Laminar Shape	ovate	Petiolar Attach.	marginal	Laminar L:W Ratio	2:1
Laminar Symmetry	symmetrical	Margin Type	crenate/erose	Lobation	unlobed

1° to 3°

1° Vein Category	basal acrodromous	2° Vein Angle	uniform
2° Vein Category	acrodromous	Inter-2° Veins	absent
Agrophic Veins	absent	3° Vein Cat.	not visible
# of Basal Veins	5	3° Vein Course	not visible
2° Vein Spacing	uniform	3° Angle to 1°	not visible

PHOTO

TEETH

# of Orders	1
Teeth/cm	3
Spacing	regular
Shape	cv cv
Sinus	rounded
Apex	simple

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Strathcona Fiord 009 | Morphotype #: 048

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 422-3886R

Localities & Specimens

422-3882, -3865, -3886 (reverse)

LEAF

Leaf Organization	simple	Base Angle	obtuse	Apex Angle	obtuse
Laminar Size	notophyll	Base Shape	truncate		
CLAMP Size	microphyll 3	Apex Shape	rounded		
Laminar Shape	elliptic	Petiolar Attach.	marginal	Laminar L:W Ratio	1:1
Laminar Symmetry	symmetrical	Margin Type	crenate	Lobation	unlobed

1° to 3°

1° Vein Category	actinodromous	2° Vein Angle	not visible
2° Vein Category	craspedodromous	Inter-2° Veins	not visible
Agrophic Veins	simple	3° Vein Cat.	not visible
# of Basal Veins	5	3° Vein Course	not visible
2° Vein Spacing	not visible	3° Angle to 1°	not visible

PHOTO

TEETH

# of Orders	1				
Teeth/cm	2				
Spacing	regular				
Shape	cv	cv			
Sinus	rounded				
Apex	simple				

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO Morphotype Name: Strathcona Fiord 010 | Morphotype #: 054

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 422-3874L

Localities & Specimens

422-3874L

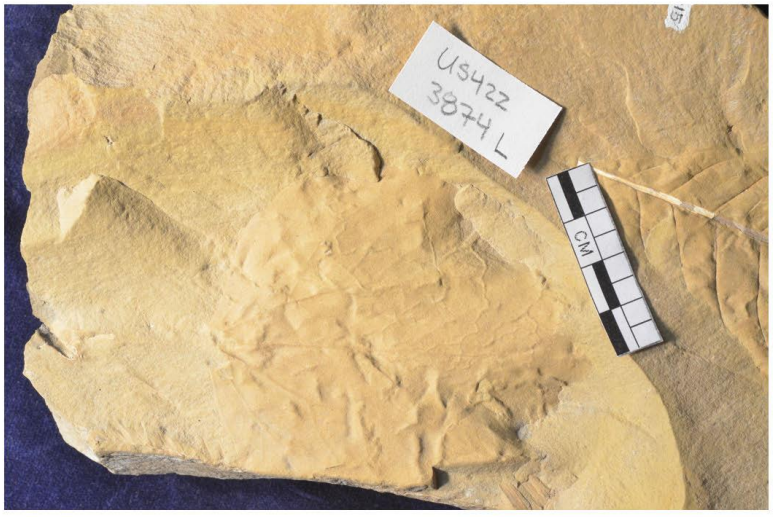
LEAF

Leaf Organization	simple	Base Angle	obtuse	Apex Angle	acute
Laminar Size	notophyll	Base Shape	rounded		
CLAMP Size	mesophyll 1	Apex Shape	convex		
Laminar Shape	ovate	Petiolar Attach.	marginal	Laminar L:W Ratio	
Laminar Symmetry	symmetrical	Margin Type	entire	Lobation	unlobed

1° to 3°

1° Vein Category	actinodromous	2° Vein Angle	uniform
2° Vein Category	craspedodromous	Inter-2° Veins	not visible
Agrophic Veins	not visible	3° Vein Cat.	not visible
# of Basal Veins	5	3° Vein Course	not visible
2° Vein Spacing	uniform	3° Angle to 1°	not visible

PHOTO



TEETH

# of Orders	n/a
Teeth/cm	
Spacing	
Shape	
Sinus	
Apex	

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Strathcona Fiord 011 | Morphotype #: 049

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 422-3886

Localities & Specimens

422-3886

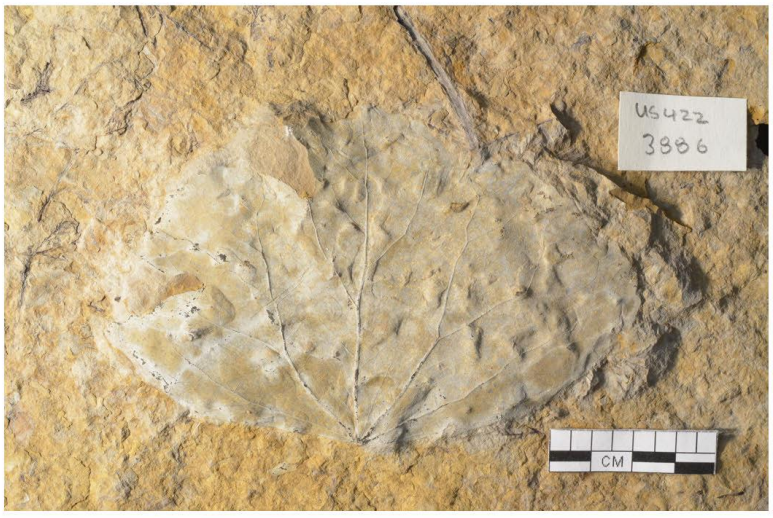
LEAF

Leaf Organization	Simple	Base Angle	obtuse	Apex Angle	obtuse
Laminar Size	mesophyll	Base Shape	truncate		
CLAMP Size	mesophyll 2	Apex Shape	rounded		
Laminar Shape	elliptic	Petiolar Attach.	marginal	Laminar L:W Ratio	1:2
Laminar Symmetry	symmetrical	Margin Type	crenate	Lobation	unlobed

1° to 3°

1° Vein Category	actinodromous	2° Vein Angle	irregular
2° Vein Category	semicraspedodromous	Inter-2° Veins	weak
Agrophic Veins	simple	3° Vein Cat.	not visible
# of Basal Veins	5	3° Vein Course	not visible
2° Vein Spacing	irregular	3° Angle to 1°	not visible

PHOTO



TEETH

# of Orders	1				
Teeth/cm	2				
Spacing	regular				
Shape	cv	cv	cv	cv	
Sinus	rounded				
Apex	simple				

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Strathcona Fiord 012 | Morphotype #: 050

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 422-3877

Localities & Specimens

422-3877

LEAF

Leaf Organization	Simple	Base Angle	wide obtuse	Apex Angle	acute
Laminar Size	mesophyll	Base Shape	cordate		
CLAMP Size	mesophyll 3	Apex Shape	acuminate		
Laminar Shape	incomplete	Petiolar Attach.	peltate ecc.	Laminar L:W Ratio	n/a
Laminar Symmetry	incomplete	Margin Type	serrate	Lobation	lobed

1° to 3°

1° Vein Category	actinodromous	2° Vein Angle	uniform
2° Vein Category	interior	Inter-2° Veins	absent
Agrophic Veins	not visible	3° Vein Cat.	mixed opp/alt
# of Basal Veins	5	3° Vein Course	convex
2° Vein Spacing	irregular	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	1
Teeth/cm	3
Spacing	regular
Shape	cv cv rt cv
Sinus	rounded
Apex	

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Strathcona Fiord 013 | Morphotype #: 051

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 422-3885

Localities & Specimens

422-3885, -3870, -3872

LEAF

Leaf Organization	simple		Base Angle	acute	Apex Angle	acute	
Laminar Size	notophyll	mesophyll	Base Shape	cuneate			
CLAMP Size	mesophyll 1	mesophyll 2	Apex Shape	acuminate			
Laminar Shape	elliptic		Petiolar Attach.	not visible	Laminar L:W Ratio	2:1	
Laminar Symmetry	symmetrical		Margin Type	serrate	Lobation	unlobed	

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	uniform
2° Vein Category	semicraspedodromous	Inter-2° Veins	absent
Agrophic Veins	not visible	3° Vein Cat.	not visible
# of Basal Veins	1	3° Vein Course	not visible
2° Vein Spacing	irregular	3° Angle to 1°	not visible

PHOTO

TEETH

# of Orders	1				
Teeth/cm	5				
Spacing	regular				
Shape	cv	st	cv	cc	
Sinus	angular				
Apex					

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Strathcona Fiord 014 | Morphotype #: 052 | Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 422-3872

Localities & Specimens

422-3872

LEAF

Leaf Organization	simple	Base Angle	wide obtuse	Apex Angle	acute
Laminar Size	microphyll	Base Shape	cordate		
CLAMP Size	microphyll 2	Apex Shape	convex		
Laminar Shape	elliptic	Petiolar Attach.	marginal	Laminar L:W Ratio	
Laminar Symmetry	symmetrical	Margin Type	entire	Lobation	unlobed

1° to 3°

1° Vein Category	actinodromous	2° Vein Angle	not visible
2° Vein Category	not visible	Inter-2° Veins	not visible
Agrophic Veins	not visible	3° Vein Cat.	not visible
# of Basal Veins	not visible	3° Vein Course	not visible
2° Vein Spacing	not visible	3° Angle to 1°	not visible

PHOTO

TEETH

# of Orders	n/a
Teeth/cm	
Spacing	
Shape	
Sinus	
Apex	

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

GENERAL INFO | Morphotype Name: Strathcona Fiord 015 | Morphotype #: 053

Major Plant Group: DIC | Organ Type: Leaf | Type Spec. #: 422-3866

Localities & Specimens

422-3866, -3869 (reverse)

LEAF

Leaf Organization	simple		Base Angle	acute	Apex Angle	acute
Laminar Size	notophyll	mesophyll	Base Shape	cuneate		
CLAMP Size	mesophyll 2		Apex Shape	convex	acuminate	
Laminar Shape	elliptic	obovate	Petiolar Attach.	marginal	Laminar L:W Ratio	2:1
Laminar Symmetry	symmetrical		Margin Type	erose	Lobation	unlobed

1° to 3°

1° Vein Category	pinnate	2° Vein Angle	uniform
2° Vein Category	weak brochidromous	Inter-2° Veins	absent
Agrophic Veins	absent	3° Vein Cat.	mixed opp/alt
# of Basal Veins	1	3° Vein Course	straight
2° Vein Spacing	irregular	3° Angle to 1°	obtuse

PHOTO

TEETH

# of Orders	n/a
Teeth/cm	
Spacing	
Shape	
Sinus	
Apex	

CUTICLE

Leaf Texture	n/a
Stomata	
Features	

	Locality						Yes = 1 No = leave blank	Notes:
	Stenkul Fiord							

Species Number	Species / Morphotypes	Lamina		Margin Character States									Size Character States								Apex Character				Base			Length to Width					Shape		
		Unlobed	Lobed	No Teeth	Teeth	Teeth Regular	Teeth Irregular	Teeth Close	Teeth Distant	Teeth Round	Teeth Acute	Teeth Compound	Compound>50%	Nanophyll	Leptophyll I	Leptophyll II	Microphyll I	Microphyll II	Microphyll III	Mesophyll I	Mesophyll II	Mesophyll III	Emarginate	Round	Acute	Attenuate	Cordate	Round	Acute	L:W <1:1	L:W 1-2:1	L:W 2-3:1	L:W 3-4:1	L:W >4:1	Obovate	Elliptic	Ovate
1	M1	1			1	1		1		1									1	1											1					1	
2	M2	1		1																					1											
3	M3	1			1	1		1			1														1											
4	M4		1		1		1	1		1									1	1				1		1				1				1		
5	M5	1			1	1	1	1			1										1				1		1	1			1				1	
6	M6		1	1	1	1		1		1												1			1		1			1						1
7	M7	1			1	1		1		1								1	1						1		1			1						1
8	M8	1			1	1		1		1		1	1					1	1						1		1			1					1	1
9	M9	1			1	1		1		1							1	1							1		1			1					1	1
10	M10	1			1	1		1		1										1			1			1				1						1
11	M11	1		1	1		1	1		1										1					1		1			1						1
12	M12	1		1																1					1											
13	M13	1			1	1		1			1											1					1				1			1		
14	M14	1			1	1		1			1											1				1				1						1
15	M15	1			1	1		1		1										1					1		1			1						1
16	M16	1			1	1		1			1											1			1			1		1					1	
17	M17	1		1																		1						1								
18	M18	1			1		1	1		1												1														
19	M19	1			1	1	1	1		1											1	1						1		1	1				1	
20	M20	1			1	1		1			1														1											
21	M21	1		1																	1				1			1		1						1
22	M22	1			1	1		1			1										1				1			1		1					1	
23	M23		1		1	1		1		1										1	1				1	1				1					1	
24	M24	1		1															1						1	1	1			1						1
25	M25	1			1		1	1			1							1	1						1	1				1						1

Status	No.	Name	Lamina Dissection	Margin Character States	Size Character States	Apex Character States	Base Character States	Length to Width Character States	Shape Character States
Unfinished	1	OK	OK	OK	OK			OK	OK
Unfinished	2	OK	OK	OK		OK			
Unfinished	3	OK	OK	OK		OK			
Finished	4	OK	OK	OK	OK	OK	OK	OK	OK
Finished	5	OK	OK	OK	OK	OK	OK	OK	OK
Finished	6	OK	OK	OK	OK	OK	OK	OK	OK
Finished	7	OK	OK	OK	OK	OK	OK	OK	OK
Finished	8	OK	OK	OK	OK	OK	OK	OK	OK
Finished	9	OK	OK	OK	OK	OK	OK	OK	OK
Finished	10	OK	OK	OK	OK	OK	OK	OK	OK
Finished	11	OK	OK	OK	OK	OK	OK	OK	OK
Unfinished	12	OK	OK	OK	OK	OK			
Unfinished	13	OK	OK	OK	OK		OK	OK	OK
Unfinished	14	OK	OK	OK	OK		OK	OK	OK
Finished	15	OK	OK	OK	OK	OK	OK	OK	OK
Finished	16	OK	OK	OK	OK	OK	OK	OK	OK
Unfinished	17	OK	OK	OK	OK		OK		
Unfinished	18	OK	OK	OK	OK				
Unfinished	19	OK	OK	OK	OK		OK	OK	OK
Unfinished	20	OK	OK	OK		OK			
Finished	21	OK	OK	OK	OK	OK	OK	OK	OK
Finished	22	OK	OK	OK	OK	OK	OK	OK	OK
Finished	23	OK	OK	OK	OK	OK	OK	OK	OK
Finished	24	OK	OK	OK	OK	OK	OK	OK	OK
Finished	25	OK	OK	OK	OK	OK	OK	OK	OK

	Locality						Yes = 1 No = leave blank	Notes:
	Split Lake							

		Lamina		Margin Character States									Size Character States									Apex Character				Base			Length to Width					Shape		
Species Number	Species / Morphotypes	Unlobed	Lobed	No Teeth	Teeth	Teeth Regular	Teeth Irregular	Teeth Close	Teeth Distant	Teeth Round	Teeth Acute	Teeth Compound	Compound<50%	Nanophyll	Leptophyll I	Leptophyll II	Microphyll I	Microphyll II	Microphyll III	Mesophyll I	Mesophyll II	Mesophyll III	Emarginate	Round	Acute	Attenuate	Cordate	Round	Acute	L:W <1:1	L:W 1-2:1	L:W 2-3:1	L:W 3-4:1	L:W >4:1	Obovate	Elliptic	Ovate
1	M1	1			1	1		1			1								1							1											
2	M2	1		1																1										1							
3	M3	1			1	1		1			1									1					1			1		1					1		
4	M4		1		1	1		1			1										1	1			1	1				1					1		
5	M5		1		1	1		1			1	1										1				1				1					1		
6	M6	1			1	1		1			1										1							1									
7	M7	1		1	1	1	1	1		1	1								1	1					1		1	1		1	1				1		
8	M8	1			1	1		1		1										1					1			1			1				1		
9	M9		1		1	1		1		1	1											1				1				1						1	
10	M10	1		1															1					1				1		1						1
11	M11	1		1															1						1			1		1						1

Status	No.	Name	Lamina Dissection	Margin Character States	Size Character States	Apex Character States	Base Character States	Length to Width Character States	Shape Character States
Unfinished	1	OK	OK	OK	OK		OK		
Unfinished	2	OK	OK	OK	OK			OK	
Finished	3	OK	OK	OK	OK	OK	OK	OK	OK
Finished	4	OK	OK	OK	OK	OK	OK	OK	OK
Finished	5	OK	OK	OK	OK	OK	OK	OK	OK
Unfinished	6	OK	OK	OK	OK		OK		
Finished	7	OK	OK	OK	OK	OK	OK	OK	OK
Finished	8	OK	OK	OK	OK	OK	OK	OK	OK
Unfinished	9	OK	OK	OK	OK		OK	OK	OK
Finished	10	OK	OK	OK	OK	OK	OK	OK	OK
Finished	11	OK	OK	OK	OK	OK	OK	OK	OK

	Locality						Yes = 1 No = leave blank	Notes:
	Strathcona							

Species Number	Species / Morphotypes	Lamina		Margin Character States								Size Character States								Apex Character			Base			Length to Width					Shape		
		Unlobed	Lobed	No Teeth	Teeth	Teeth Regular	Teeth Irregular	Teeth Close	Teeth Distant	Teeth Round	Teeth Acute	Teeth Compound	Compound<50%	Nanophyll	Leptophyll I	Leptophyll II	Microphyll I	Microphyll II	Microphyll III	Mesophyll I	Mesophyll II	Mesophyll III	Emarginate	Round	Acute	Attenuate	Cordate	Round	Acute	L:W <1:1	L:W 1-2:1	L:W 2-3:1	L:W 3-4:1	L:W >4:1	Obovate	Elliptic	Ovate
1	M1		1		1		1		1	1												1				1									1	
2	M2	1		1																		1			1			1			1	1			1	
3	M3	1			1	1		1			1								1						1		1			1						1
4	M4	1			1		1	1		1											1				1	1				1						1
5	M5	1		1	1		1		1	1	1									1					1						1					1
6	M6	1		1	1	1			1	1												1						1								1
7	M7	1			1	1		1			1							1						1												1
8	M8	1		1	1	1			1	1									1					1								1				1
9	M9	1			1	1		1		1									1							1			1							1
10	M10		1	1																1						1								1	
11	M11	1			1	1		1			1										1					1								1	
12	M12		1		1	1		1			1											1			1	1			1							1
13	M13	1			1		1		1		1									1	1				1					1				1	
14	M14	1		1														1								1			1						1
15	M15	1		1																	1			1				1							

Status	No.	Name	Lamina Dissection	Margin Character States	Size Character States	Apex Character States	Base Character States	Length to Width Character States	Shape Character States
Unfinished	1	OK	OK	OK	OK		OK		OK
Finished	2	OK	OK	OK	OK	OK	OK	OK	OK
Finished	3	OK	OK	OK	OK	OK	OK	OK	OK
Finished	4	OK	OK	OK	OK	OK	OK	OK	OK
Unfinished	5	OK	OK	OK	OK	OK		OK	OK
Unfinished	6	OK	OK	OK	OK	OK			OK
Unfinished	7	OK	OK	OK	OK	OK			OK
Unfinished	8	OK	OK	OK	OK	OK		OK	OK
Unfinished	9	OK	OK	OK	OK		OK	OK	OK
Unfinished	10	OK	OK	OK	OK		OK		OK
Unfinished	11	OK	OK	OK	OK		OK		OK
Finished	12	OK	OK	OK	OK	OK	OK	OK	OK
Unfinished	13	OK	OK	OK	OK	OK		OK	OK
Unfinished	14	OK	OK	OK	OK		OK	OK	OK
Unfinished	15	OK	OK	OK	OK	OK	OK		

locality: Stenkul Fiord		leaf size (MLA)										leaf margin		
TAXON	specimens	Leptophyll	Nanophyll	Microphyll	Notophyll	Mesophyll	Macrophyll	minLn	maxLn	MLn		Morphotype	number of specimens scored	non-toothed
M001	2	0	0	0.5	0.5	0	0	2025	4500	8.1		M001	2	0
M002	1	0	0	0	0	0	0					M002	1	1
M003	1	0	0	0	0	0	0					M003	1	0
M004	4	0	0	0.5	0.5	0	0	2025	4500	8.1		M004	4	0
M005	4	0	0	0	1	0	0	4500	4500	8.4		M005	4	0
M006	3	0	0	0	0	1	0	18225	18225	9.8		M006	3	0.5
M007	3	0	0	1	0	0	0	2025	2025	7.6		M007	3	0
M008	5	0	0	1	0	0	0	2025	2025	7.6		M008	5	0
M009	5	0	0.5	0.5	0	0	0	225	2025	7.0		M009	5	0
M010	2	0	0	0	1	0	0	4500	4500	8.4		M010	2	0
M011	6	0	0	0	1	0	0	4500	4500	8.4		M011	6	0.5
M012	1	0	0	0	1	0	0	4500	4500	8.4		M012	1	1
M013	1	0	0	0	0	1	0	18225	18225	9.8		M013	1	0
M014	1	0	0	0	0	1	0	18225	18225	9.8		M014	1	0
M015	3	0	0	0	1	0	0	4500	4500	8.4		M015	3	0
M016	1	0	0	0	0	1	0	18225	18225	9.8		M016	1	0
M017	3	0	0	0	0	1	0	18225	18225	9.8		M017	3	1
M018	1	0	0	0	0	1	0	18225	18225	9.8		M018	1	0
M019	3	0	0	0	0.5	0.5	0	4500	18225	9.3		M019	3	0
M020	1	0	0	0	0	0	0					M020	1	0
M021	1	0	0	0	1	0	0	4500	4500	8.4		M021	1	1
M022	1	0	0	0	1	0	0	4500	4500	8.4		M022	1	0
M023	8	0	0	0	1	0	0	4500	4500	8.4		M023	8	0
M024	1	0	0	1	0	0	0	2025	2025	7.6		M024	1	1
M025	2	0	0	1	0	0	0	2025	2025	7.6		M025	2	0
25	64	0.0%	2.0%	22.0%	38.0%	26.0%	0.0%			8.6				
													64	24%
										number of leaf morphotypes =	25		LMP =	0.24

locality: Strathcona Fiord				leaf size (MLA)								leaf margin		
TAXON	specimens	Leptophyll	Nanophyll	Microphyll	Notophyll	Mesophyll	Macrophyll	minLn	maxLn	MLn		Morphotype	number of specimens scored	non-toothed
SF1	2	0	0	0	0	1	0	18225	18225	9.8		SF1	2	0
SF2	1	0	0	0	0	1	0	18225	18225	9.8		SF2	1	1
SF3	3	0	0	1	0	0	0	2025	2025	7.6		SF3	3	0
SF4	3	0	0	0	1	0	0	4500	4500	8.4		SF4	3	0
SF5	3	0	0	0	1	0	0	4500	4500	8.4		SF5	3	0.5
SF6	1	0	0	0	0	1	0	18225	18225	9.8		SF6	1	0.5
SF7	2	0	0	1	0	0	0	2025	2025	7.6		SF7	2	0
SF8	2	0	0	1	0	0	0	2025	2025	7.6		SF8	2	0.5
SF9	3	0	0	1	0	0	0	2025	2025	7.6		SF9	3	0
SF10	1	0	0	0	1	0	0	4500	4500	8.4		SF10	1	1
SF11	1	0	0	0	1	0	0	4500	4500	8.4		SF11	1	0
SF12	1	0	0	0	0	1	0	18225	18225	9.8		SF12	1	0
SF13	3	0	0	0	1	0	0	4500	4500	8.4		SF13	3	0
SF14	1	0	0	1	0	0	0	2025	2025	7.6		SF14	1	1
SF15	2	0	0	0	1	0	0	4500	4500	8.4		SF15	2	1
15	29	0.0%	0.0%	33.3%	40.0%	26.7%	0.0%			8.5				
													29	37%
										number of leaf morphotypes =	15		LMP =	0.37

locality: Split Lake		leaf size (MLA)										leaf margin		
TAXON	specimens	Leptophyll	Nanophyll	Microphyll	Notophyll	Mesophyll	Macrophyll	minLn	maxLn	MLn		Morphotype	number of specimens scored	non-toothed
SL01	1	0	0	1	0	0	0	2025	2025	7.6		SL01	1	0
SL02	1	0	0	0	1	0	0	4500	4500	8.4		SL02	1	1
SL03	3	0	0	0	1	0	0	4500	4500	8.4		SL03	3	0
SL04	4	0	0	0	0.5	0.5	0	4500	18225	9.3		SL04	4	0
SL05	1	0	0	0	0	1	0	18225	18225	9.8		SL05	1	0
SL06	1	0	0	0	1	0	0	4500	4500	8.4		SL06	1	0
SL07	5	0	0	0.5	0.5	0	0	2025	4500	8.1		SL07	5	0.5
SL08	1	0	0	0	1	0	0	4500	4500	8.4		SL08	1	0
SL09	2	0	0	0	0	1	0	18225	18225	9.8		SL09	2	0
SL10	1	0	0	1	0	0	0	2025	2025	7.6		SL10	1	1
SL11	1	0	0	1	0	0	0	2025	2025	7.6		SL11	1	1
11	21	0.0%	0.0%	31.8%	45.5%	22.7%	0.0%			8.5				
													21	32%
										number of leaf morphotypes =	11		LMP =	0.32

Appendix B:

Supplemental Data for Chapter 3

1. Stenkul Fiord Area

1.1 Stenkul Fiord

USPC 430-439 – 77.35 -83.59

Equisetum sp., *Metasequoia occidentalis, Elatocladus cordillera*, CAF-133, *Nordenskioldia borealis, Archeampelos* cf. *A. acerifolia, Trochodendroides arctica, Trochodendroides curvidens, Trochodendroides crenulata, Trochodendroides richardsonii, Vitiphyllum* cf. *V. sewardii*, cf. *Paracarpinus* sp., *Ushia* cf. *U. olafsenii*, cf. '*Carya' antiquorum, Ulmus ulmifolia, Aesculus longipedunculus*, cf. *Cornophyllum* sp., CAF-016, CAF-024, CAF-025, CAF-033, CAF-134, CAF-086, CAF-137, CAF-142, CAF-140, CAF-141

USPC 1005 – 77.3374 -83.5468

Metasequoia occidentalis, Glyptostrobus nordenskioldii, Archeampelos cf. *A. acerifolia, Trochodendroides* sp., *Vitiphyllum* cf. *V. sewardii, Ushia* cf. *U. olafsenii, Aesuculus longipedunculus, Macginitiea* cf *M. nobilis*

USPC 1012 – 77.3530 -83.6314

Metasequoia occidentalis, Glyptostrobus nordenskioldii, Archeampelos cf. *A. acerifolia, Trochodendroides* sp., *Vitiphyllum* cf. *V. sewardii, Ushia* cf. *U. olafsenii, Aesculus longipedunculus***,** *Macginitiea* cf. *M. nobilis*

USPC 1014 – 77.3487 -83.4441

Metasequoia occidentalis, Glyptostrobus nordenskioldii, Trochodendroides sp., *Vitiphyllum* cf. *V. sewardii, Ushia* cf. *U. olafsenii, Aesculus longipedunculus, Ulmus ulmifolia*

YPM 7973, 8410-8418, 8421 & 8426, 848 – Precise location information is not available for these localities.

Salvinia cf. *S. preauriculata, Ginkgo adiantoides, Metasequoia occidentalis, Glyptostrobus nordenskioldii, Zingiberopsis* cf. *Z. isonervosa,* cf. *Nelumbo* sp., *Macginitiea* aff. M. *nobilis, Archeampelos* cf. *A. acerifolia, Nyssidium arcticum, Vitiphyllum* cf. *V. sewardii, Comptonia* sp., *Ulmus ulmifolia,* CAF-073, CAF-100, CAF-123

1.2 Swinnerton Peninsula – 77.31 -81.57

YPM 8422, 8423, 8545-8547 – Precise location information is not available for these YPM localities

CAF-096, cf. *Nelumbo* sp., *Macginitiea* cf. *M. nobilis, Macginicarpa* cf. *M. manchesteri,* cf. *Paracarpinus* sp., cf. *Sorbaria* aff. *S. wahrhaftigii, Ulmus ulmifolia,* cf. *Cornophyllum* sp.

1.3 Split Lake

USPC 441-444 – 77.87 -81.62

Equisetum sp., *Metasequoia occidentalis, Glyptostrobus nordenskioldii, Trochodendroides arctica, Trochodendroides crenulata, Vitiphyllum* cf. *V. sewardii, Craspedodromophyllum* cf. *C. malmgrenii, Ushia* cf. *U. olafsenii, Quereuxia angulata,* CAF-016, CAF-104, CAF-086

2. Strand Fiord

2.1 Strand Fiord

USPC 162 – 79.2466 -91.2292

Equisetum sp.

USPC 163 – 79.2722 -91.4399

Ginkgo adiantoides, Metasequoia occidentalis, Magnolia sp., *Trochodendroides arctica, Trochodendroides curvidens, Trochodendroides crenulata, Trochodendroides richardsonii, Aesculus longipedunculus*

USPC 164 – 79.2406 -91.4353

Metasequoia occidentalis, Comptonia sp., *Ulmus ulmifolia*

USPC 165 – 79.2466 -91.2292

Nyssidium arcticum

USPC 166 – 79.2466 -91.2292

Trochodendroides arctica, Trochodendroides curvidens, Ushia cf. *U. olafsenii*, CAF-152

USPC 167 – 79.2466 -91.2292

Archeampelos cf. *A. acerifolia*

USPC 168 – 79.2482 -91.1394

Equisetum sp., *Macginitiea* aff. *M. nobilis, Trochodendroides arctica, Macclintockia* sp.

USPC 169 – 79.2490 -91.1295

Archeampelos cf. *A. acerifolia, Nyssidium arcticum, Trochodendroides* arctica, *Trochodendroides crenulata, Trochodendroides richardsonii, Aesculus longipedunculus, Quereuxia angulata*, CAF-143

USPC 170 – 79.2490 -91.1295

Trochodendroides arctica, Trochodendroides richardsonii

USPC 171 – 79.2461 -91.2339

CAF-151

USPC 172 – 79.2516 -91.2386

Trochodendroides crenulata, Ushia cf. *U. olafsenii*

USPC 173 – 79.2474 -91.2538

Archeampelos cf. *A. acerifolia, Trochodendroides arctica, Trochodendroides richardsonii, Vitiphyllum* cf. *V. sewardii*

USPC 174 – 79.2609 -91.2429

Archeampelos cf. *A. acerifolia*, *Vitiphyllum* cf. *V. sewardii*, cf. ‘*Carya’ antiquorum*

USPC 175 – 79.2503 -91.0390

Coniopteris blomstrandii, *Metasequoia occidentalis*, *Trochodendroides crenulata*, *Trochodendroides richardsonii*, *Ushia* cf. *U. olafsenii*, cf. ‘*Carya’ antiquorum*, *Aesculus longipedunculus*, CAF-073, CAF-104

USPC 176 – 79.2503 -91.0390

cf. ‘*Carya’ antiquorum*

USPC 177 – 79.2593 -91.0261

Averrhoites cf. *A. affinis*

USPC 178 – 79.2554 -91.0304

Metasequoia occidentalis, *Archeampelos* cf. *A. acerifolia*, *Vitiphyllum* cf. *V. sewardii*, cf. ‘*Carya’ antiquorum*, *Averrhoites* cf. *A. affinis*

USPC 179 – 79.2721 -91.0304

Archeampelos cf. *A. acerifolia*, *Vitiphyllum* cf. *V. sewardii*

YPM 7920 – Precise location information is not available for this YPM locality.

Osmunda macrophylla, *Metasequoia occidentalis*, *Zingiberopsis* cf. *Z. isonervosa*, cf. *‘Carya’ antiquorum*, *Averrhoites* cf. *A. affinis*

3. Strathcona Fiord Area

3.1 Strathcona Fiord

USPC 422 – 78.5727 -82.9808

Metasequoia occidentalis, Tetracentron cf. *T. hopkinsii, Trochodendroides* sp., *Vitiphyllum* cf. *V. sewardii, Alnus* sp., *Ushia* cf. *U. olafsenii, Aesculus longipedunculus*

3.2 Taggart River

USPC 358 – 78.6322 -81.9092

Quereuxia angulata

USPC 359 – 78.6310 -81.8975

Quereuxia angulata

USPC 360 – 78.6303 -81.9323

Quereuxia angulata

USPC 361 – 78.6275 -81.9198

Equisetum sp., *Quereuxia angulata*

USPC 362 – 78.6067 -81.7835

Quereuxia angulata

USPC 363 – 78.6377 -81.9392

Quereuxia angulata, CAF-016

USPC 367 – 78.6475 -81.9473

Metasequoia occidentalis, *Macginitiea* aff. *M. nobilis*, cf. *Platanus* sp., *Nyssidium arcticum*, *Vitiphyllum* cf. *V. sewardii*, *Corylites hebridicus*, *Fagopsiphyllum* cf. *F. groenlandicum*, cf. *Crataegus* sp. 2, *Quereuxia angulata*

USPC 369 – 78.6482 -81.9445

Corylites hebridicus

USPC 370 – 78.6477 -81.9580

Quereuxia angulata

USPC 371 – 78.6445 -81.9120

Metasequoia occidentalis, Nyssidium arcticum, Corylites hebridicus, Ushia cf. *U. olafsenii*

3.3 Bay Fiord – 78.83 -82.29 – Precise location information is not available for these YPM localities.

YPM 7950

Glyptostrobus nordenskioldii, cf. *Nelumbo* sp., *Macginitiea* cf. *M. nobilis*

YPM 7962

CAF-103

YPM 7969

Metasequoia occidentalis

YPM 7971

Quereuxia angulata

YPM 8437

CAF-070

YPM 8439

Ginkgo adiantoides, Macginitiea aff. M. *nobilis*

YPM 8441

Glyptostrobus nordenskioldii, CAF-076

3.4 Matthew Peninsula – 78.78 -82.53

YPM 8518 – Precise location information is not available for this YPM locality.

cf. *Cunninghamia* sp.

4. Fosheim South

4.1 Petrocan Locality

USPC 23-26 – 79.74 -85.58

Metasequoia occidentalis, Glyptostrobus nordenskioldii, CAF-139, *Corylites hebridicus, Ushia* cf. *U. olafsenii, Quereuxia angulata*

4.2 Fosheim Anticline

USPC 111 – 79.7337 -84.8137

Equisetum sp., *Ginkgo adiantoides, Metasequoia occidentalis*, *Glyptostrobus nordenskioldii*, *Elatocladus cordillera*, *Magnolia* sp., *Platanus* sp., Nordenskioldia *borealis*, *Nyssidium arcticum*, *Trochodendroides arctica*, *Trochodendroides curvidens, Trochodendroides crenulata*, *Trochodendroides richardsonii*, CAF-144, *Corylites hebridicus*, *Craspedodromophyllum* cf. *C. malmgrenii*, *Fagopsiphyllum* cf. *F. groenlandicum, Ushia* cf. *U. olafsenii*, cf. '*Carya' antiquorum, Ulmus ulmifolia*, *Aesculus longipedunculus*, aff. *Celastrinites* sp., CAF-132, CAF-086, CAF-124, CAF-146, CAF-145

4.3 Fosheim Peninsula

USPC 250 – 79.7005 -84.2912

Glyptostrobus nordenskioldii, Corylites hebridicus, Ushia cf. *U. olafsenii*

USPC 251 – 79.7005 -84.2912

Equisetum sp., *Metasequoia occidentalis, Glyptostrobus nordenskioldii*, *Cupressinocladus* sp. 2, *Nyssidium arcticum, Trochodendroides arctica, Trochodendroides crenulata, Corylites hebridicus, Ushia* cf. *U. olafsenii*

USPC 253 – 79.6972 -84.2700

Ushia cf. *U. olafsenii, Quereuxia angulata*

USPC 255 – 79.7362 -85.1467

Metasequoia occidentalis, Glyptostrobus nordenskioldii, Trochodendroides arctica, Corylites hebridicus, Ushia cf. *U. olafsenii*

USPC 259 – 79.7162 -85.2317

Glyptostrobus nordenskioldii, Alnus cf. *A. parvifolia, Alnus* sp., *Ushia* cf. *U. olafsenii, Ulmus ulmifolia*

YPM 7936, 7937, 8432 – Precise location information does not exist for these YPM localities.

YPM 7936

Metasequoia occidentalis

YPM 7937

Equisetum sp., *Glyptostrobus nordenskioldii, Cupressinocladus* sp. 1, *Fagopsiphyllum* cf. *F. groenlandicum*

YPM 8432

Metasequoia occidentalis, CAF-085, CAF-063

5. Fosheim North

5.1 Ox-Head Creek

US 6 – 79.9372 -84.9906

Metasequoia occidentalis, Zingiberopsis cf. *isonervosa, Archeampelos* cf. *A. acerifolia, Trochodendroides arctica, Trochodendroides curvidens, Trochodendroides crenulata, Fagopsiphyllum* cf. *F. groenlandicum, Ushia* cf. *U. olafsenii, Aesculus longipedunculus,* CAF-086

USPC 22 – 79.9372 -84.9906

Equisetum sp., *Osmunda macrophylla, Coniopteris blomstrandii, Metasequoia occidentalis, Glyptostrobus nordenskioldii, Tetracentron* cf. *T. hopkinsii, Trochodendroides arctica, Trochodendroides curvidens, Trochodendroides crenulata, Trochodendroides richardsonii*, cf. *Paracarpinus* sp., *Corylites hebridicus, Ushia* cf. *U. olafsenii*, *Ulmus ulmifolia*, CAF-138

5.2 Mosquito Creek

USPC 100 – 79.9470 -84.7222

Zingiberopsis cf. *Z. isonervosa*

USPC 101 – 79.9430 -84.7633

Equisetum sp., *Thuja polaris*

USPC 102 – 79.9387 -84.7547

Equisetum sp., *Cupressinocladus* sp. 2

USPC 195 – 79.9547 -84.7105

Aesculus longipedunculus

USPC 196 – 79.9520 -84.7492

Metasequoia occidentalis, Archeampelos cf. *A. acerifolia, Trochodendroides arctica, Trochodendroides crenulata, Trochodendroides richardsonii, Vitiphyllum* cf. *V. sewardii*, *Craspedodromophyllum* cf. *C. malmgrenii, Ushia* cf. *U. olafsenii,* CAF-086

USPC 198 – 79.9430 -84.7633

Equisetum sp., *Ushia* cf. *U. olafsenii*, CAF-086

USPC 200 – 79.9458 -84.7263

Metasequoia occidentalis, Archeampelos cf. *A. acerifolia, Trochodendroides arctica, Trochodendroides curvidens, Trochodendroides crenulata, Trochodendroides richardsonii*, CAF-144, *Vitiphyllum* cf. *V. sewardii, Corylites hebridicus*, *Craspedodromophyllum* cf. *C.*

malmgrenii, Fagopsiphyllum cf. *F. groenlandicum, Ushia* cf. *U. olafsenii, Ulmus ulmifolia, Aesculus longipedunculus,* CAF-130

5.3 Remus Creek

USPC 191 & 193 – 79.9885 -85.0178

Ushia cf. *U. olafsenii, Quereuxia angulata*

5.4 Hot Weather Creek

USPC 104, 105, 108 – 79.94 -84.47

Equisetum sp., *Osmunda macrophylla, Metasequoia occidentalis, Zingiberopsis* cf. *Z. isonervosa, Trochodendroides arctica, Trochodendroides crenulata, Trochodendroides richardsonii, Fagopsiphyllum* cf. *F. groenlandicum, Ushia* cf. *U. olafsenii, Ulmus ulmifolia, Aesculus longipedunculus,* CAF-086

5.5 Slidre River

USPC 657 & 661 – 79.8592 -84.5242

Metasequoia occidentalis, Vitiphyllum cf. *V. sewardii, Ushia* cf. *U. olafsenii*

6. Judge Daly Promontory

6.1 Franklin Pierce Outlier

USPC 716 & 718 – 79.52 -74.54

Ushia cf. *U. olafsenii*

6.2 Carl Ritter Bay

USPC 708, 710-712, & 715 – 80.99 -66.90

Equisetum sp., *Metasequoia occidentalis, Glyptostrobus nordenskioldii, Vitiphyllum* cf. *V. sewardii, Ushia* cf. *U. olafsenii,* CAF-086

6.3 Pavy River

USPC 752-759 – 81.4813 -64.9400

Equisetum sp., *Osmunda macrophylla*, *Coniopteris blomstrandii*, *Metasequoia occidentalis*, *Glyptostrobus nordenskioldii*, *Cupressinocladus* sp. 2, *Nyssidium arcticum*, *Alnus* cf. *A. parvifolia*, *Ushia* cf. U. *olafsenii*, cf. *Crataegus* sp. 1, CAF-086

7. Lake Hazen

7.1 Lake Hazen

USPC 261 – 81.80 -71.82

Equisetum sp., *Ginkgo adiantoides*, *Glyptostrobus nordenskioldii*, CAF-148, *Magnolia* sp., *Nordenskioldia borealis*, *Archeampelos* cf. *A. acerifolia*, *Nyssidium arcticum*, *Trochodendroides arctica*, *Trochodendroides richardsonii*, *Vitiphyllum* cf. *V. sewardii*, *Corylites hebridicus*, *Ushia* cf. *U. olafsenii*, cf. '*Carya' antiquorum*, *Aesculus longipedunculus*, aff. *Celastrinites* sp., CAF-147, CAF-093

USPC 267 – 81.9656 -69.6278

Glyptostrobus nordenskioldii, *Alnus* cf. *A. parvifolia*, *Ushia* cf. *U. olafsenii*

USPC 268 – 81.9683 -69.6101

Metasequoia occidentalis

USPC 275 – 82.0204 -69.7415

Coniopteris blomstrandii, *Metasequoia occidentalis*, *Vitiphyllum* cf. *V. sewardii*, *Alnus* sp.

Appendix C:

Supplemental Data for Chapter 4

Supporting Material and Methods

Material and Methods

Paleobotany collection methods.

Palynology.

Diversity analyses.

Geological section measurements.

Fig S1–S3

Table S1–S9

References (34–50)

Paleobotany collection methods

Fossil megaflora (e.g., leaves, fruits, seeds) were census collected from discrete horizons in measured sections (see geological measurement section below) at Stenkul Fiord on southern Ellesmere Island. The census method requires that all fossil specimens within a horizon be recorded to minimize collection bias, which typically arises from collecting only well-preserved, complete, or novel specimens (*4–5*, *34–35*). Approximately 300 specimens—typically dicotyledonous angiosperm leaf compression fossils—are required to accurately reconstruct diversity patterns from fossil leaf floras (*34–35*). Over the course of the 2017 field season at Stenkul Fiord approximately 740 leaf compression fossils were collected from two sedimentary horizons with stratigraphic context.

Fossils were counted and photographed in the field and grouped based on the morphotypes established in West et al. (*12*), which allowed for identification of poorly preserved or fragmented specimens. A conservative lumping approach was followed as certain morphotypes (i.e., *Trochodendroides* sp.) could not be reliably sorted into distinct groups based on leaf venation, size, or shape alone; thus, fossil leaves attributed to that group were counted a single morphotype.

375 compression fossils were collected from fossil locality USPC-1005, 317 (84%) of those fossils were dicotyledonous angiosperms. 365 compression fossils were collected from fossil locality USPC-1014, 207 (56%) of those fossils were dicotyledonous angiosperms (see Table S1 for counts). The recommended ~300 specimens for locality USPC-1014 was not achieved due to time constraints. Fossils were returned to the University of Saskatchewan for additional study and photographed as part of the University of Saskatchewan Paleobotany Collection (USPC). The final repository of these fossils will be the Canadian Museum of Natural History as part of the Nunavut Paleobotany Collection (NPC).

Additional collections of leaf compression fossil megaflora from the Margaret Formation at Stenkul Fiord are housed in the USPC collected by James Basinger, and also

collections housed in the Yale Peabody Museum of Natural History collected by the late Leo Hickey. These collections were available for this study, but were not used. Precise location data for the Hickey collections was not readily available, and as such many of these localities could not be relocated during field site reconnaissance in 2017. Further, in some cases, these megaflora collections were not census sampled (i.e., the previously existing USPC collections), which could potentially introduce collector's bias into the diversity analyses, and thus could not produce comparable data. These situations negated the utility of using the prior collections for our goal of exploring Arctic plant diversity during the early Eocene hyperthermals. The present study was therefore restricted to purpose-collected samples from the 2017 field work at Stenkul Fiord, as these were census collected and could be well-constrained within the recently developed lithostratigraphy.

Palynology

Palynological analysis was conducted on the strata that preserved the megaflora collections studied here. The nearest stratigraphic coal layer was also sampled to eliminate potential taphonomic bias on the palynoassemblage. Terrestrial depositional environments (e.g., swamps) typically represent local vegetation with varying degrees of regional pollen rain (*36*).

Mudstones and coals were prepared for palynological analysis following standard techniques (*37*–*39*) by Global Geolab Limited (729B 15th Street, Medicine Hat, Alberta, Canada, T1A 4W7). Palynomorph processing included washing, acid digestion with HCl and HF, oxidation with Schulze's solution, staining with Safranin O, and permanent mounting with liquid bioplastic. Microscope slides made from the coals are stored at the Geological Survey of Canada, Calgary, Alberta, on loan from the Geological Survey of Canada and Canadian Museum of Nature collections. Microscope slides prepared from mudstone samples are stored at Brandon University, Brandon, Manitoba on loan from Canadian Museum of Nature. All

microscope slides are currently on loan from the Canadian Museum of Natural History as part of the Nunavut Paleobotany Collection (NPC).

Quantitative palynological analysis was based on minimum counts of 400 pollen and spore grains from obligately terrestrial plants on unsieved sample preparations. Pollen and spores were identified to the lowest possible taxonomic classification. See Table S2 for count data.

Diversity analyses

Rarefaction down samples larger datasets to a standardized size of specimens or individuals, typically the smallest sample set available, so that each sample may be evaluated in equal terms (*40–41*). Classical rarefaction can underestimate the diversity of highly diverse assemblages by compressing relative richness and artificially flattening diversity curves (*40*). This can be resolved by standardizing a sample to equal levels of completeness, a method that reconstructs richness with high accuracy (*42–43*).

This approach was expanded to include extrapolation and called coverage-based rarefaction (*23*). Sample coverage, essentially the measure of sample completeness, gives the proportion of individuals that belong to a species in the original population. The 'coverage deficit', calculated by subtracting coverage from unity, indicates the proportion of individuals in the source population that remain unsampled. The coverage deficit also corresponds to the probability that a previously unsampled species would be found from continued sampling effort (*23*). For example, if the coverage of a sample is estimated to be 75%, then the coverage deficit is 100% - 75% = 25%. Thus, there is a 25% probability that a new species would be found if the sample were enlarged by one specimen (*23*). These numbers provide an objective measure of sample completeness, therefore, diversity may be efficiently estimated from a sufficiently large sample and the frequencies of rare species therein. For example, when a sample has a high number of singletons, the sample is considered to be poorly sampled; however, when a low

number of singletons are present, the sample is considered to be well-sampled or has a high measure of sample completeness (*23*).

Coverage-based rarefaction was extended to include Hill numbers (*24*), which essentially equate to the effective number of species, as these numbers are also dependent upon sample size and inventory completeness. The Hill numbers are specified by diversity order q, which determines how sensitive each rank is to species relative abundances, and are dependent on sample size and inventory completeness (*25*). The Hill numbers include three well-known metrics for assessing species diversity; species richness, where $q = 0$; the exponential of the Shannon index and referred to as Shannon diversity, where $q = 1$; and, Simpson's diversity, where $q = 2$ (*24-25*).

Species richness ($q = 0$) counts species equally but without consideration of their relative abundance. Shannon diversity ($q = 1$) counts individuals equally, as such species are considered to be counted in proportion to their abundances. Thus, Shannon diversity can be interpreted as the effective number of common species in an assemblage (*25*). Simpson diversity ($q = 2$) counts only the dominant species of an assemblage and can be interpreted as the effective number of dominant species in a sample (*25*).

The program iNEXT (*25*) was used to generate rarefaction/extrapolation for both macro- and microfloral assemblages (Figures S1-S3) in the program R (*44*). The curves use abundance data and interpolate/extrapolate based on sample size and coverage. Sample-completeness curves were also generated in order to assess how the completeness of each megaflora. Samples are extrapolated to the double the minimum sample size, and bootstrapped to 95% confidence intervals (*23*), generated as part of the iNEXT program (*25*). Furthermore, we provide the Hill number ($q = 0, 1, 2$; Tables S3-S8) diversity indices for each locality, as well as more traditional calculations of the Simpon's Index and Shannon Diversity and Evenness Index to assess the diversity and evenness of each macrofloral assemblage (Table S9).

Fossil leaf and pollen and spore assemblages were compared against modern forest data collected and identified in similar processes so as to produce comparable data. Modern leaf data were sourced from prior studies that compared fossil and modern leaf assemblages (*1*, *45*). The Harvard Forest modern leaf data was collected by S.B Archibald. Honey Hill South Carolina, Gainesville Florida, and Namekus Lake, Prince Albert National Park, Saskatchewan were collected by D.R Greenwood.

Modern pollen data were sourced from the North American pollen database (*46*), and sites were selected based on their geographical similarity to the modern leaf litter data. Sources include Camel Lake Florida (*47*), Dismal Swamp Virginia (*48*), Rockyhock Bay, North Carolina (*49*), and Cranberry Glades, Appalachia (*50*).

Geological section measurements

The Margaret Formation was affected by syn-sedimentary and post-depositional tectonics associated with Eurekan deformation and has resulted in a complicated pattern of folds, faults, thrusts, and unconformities (*21*). A new geological map based on interpretations of high-resolution satellite images, aerial photographs, and field verifications, was compiled for the SW end of Stenkul Fiord (*21*). Sections were georeferenced by a handheld GPS unit.

The lithostratigraphy of four sections at Stenkul Fiord were measured and described (Figure 1). Section S1 is situated at the southwestern end of Stenkul Fiord along the NE-facing outcrop slope and section S3 along the N-facing outcrop slope in the main W-E valley there (cf. geological map in *21*). Section S5 is located just outside the new geological map at the opposing eastern shore of Stenkul Fiord.

Sections S1 and S3 are well correlated by the mapped and dated volcanic ash layer MA-1 (*21*). Section S5 on the other side of the fiord is likely offset from sections S1 and S3 by a fault. Section S5 probably represents stratigraphically older units of the Margaret Formation (cf. lateral correlations in *14*, *17*), likely of late Paleocene age (*21*).

The predominantly fluvial deposits of the Margaret Formation are comprised of mudstones and siltstones and sandstones of predominantly medium to coarse grain size with numerous intercalated coal seams (cf. *17, 21*). In general, the sediments are weakly consolidated. Leaf megafossils are preserved in rare carbonate cemented silt- and mudstones.

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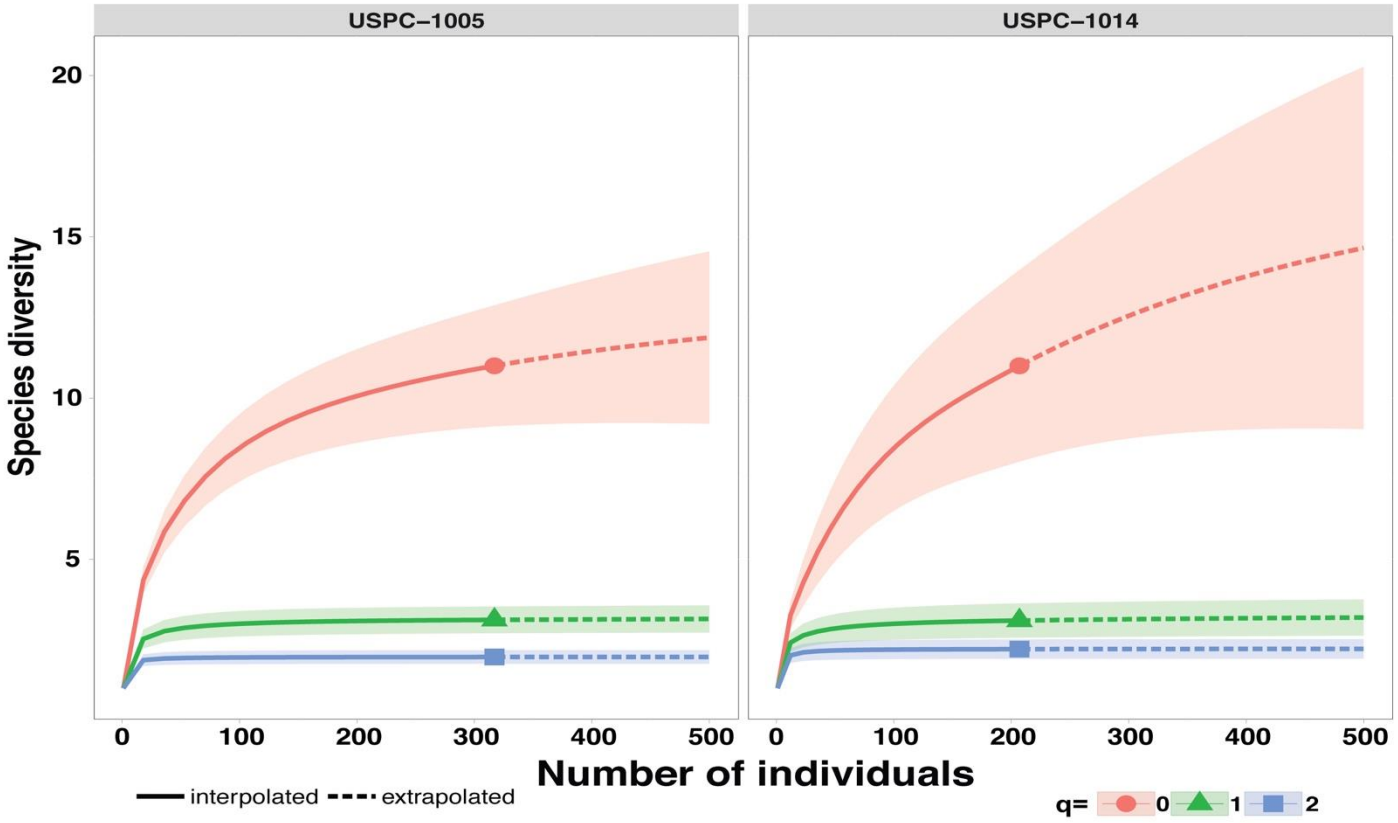

Figure S1: Shows curves for each Hill number (q = 0, 1, 2) for the census sampled leaf megaflora localities USPC-1005 and USPC-1014. The first curve (q = 0) is a classical rarefaction curve (also found in the main document). The second curve represents a rarefaction curve based on the Shannon Diversity Index (q = 1) and shows interpolated number of common species inherent to the fossil collection, the dashed line shows the extrapolated number of common species were the sample size to increase. This curve does not rise in number, suggesting that the common elements of the fossil locality have already been identified. The third curve represents a curve based on Simpsons Diversity (q = 2) and shows the interpolated number of dominant species, the dashed line shows the extrapolated number of dominant species if the sample number were to increase. Similar to that of the Shannon diversity curve, the asymptote has already been reached and no new dominant morphotypes are predicted to be found.

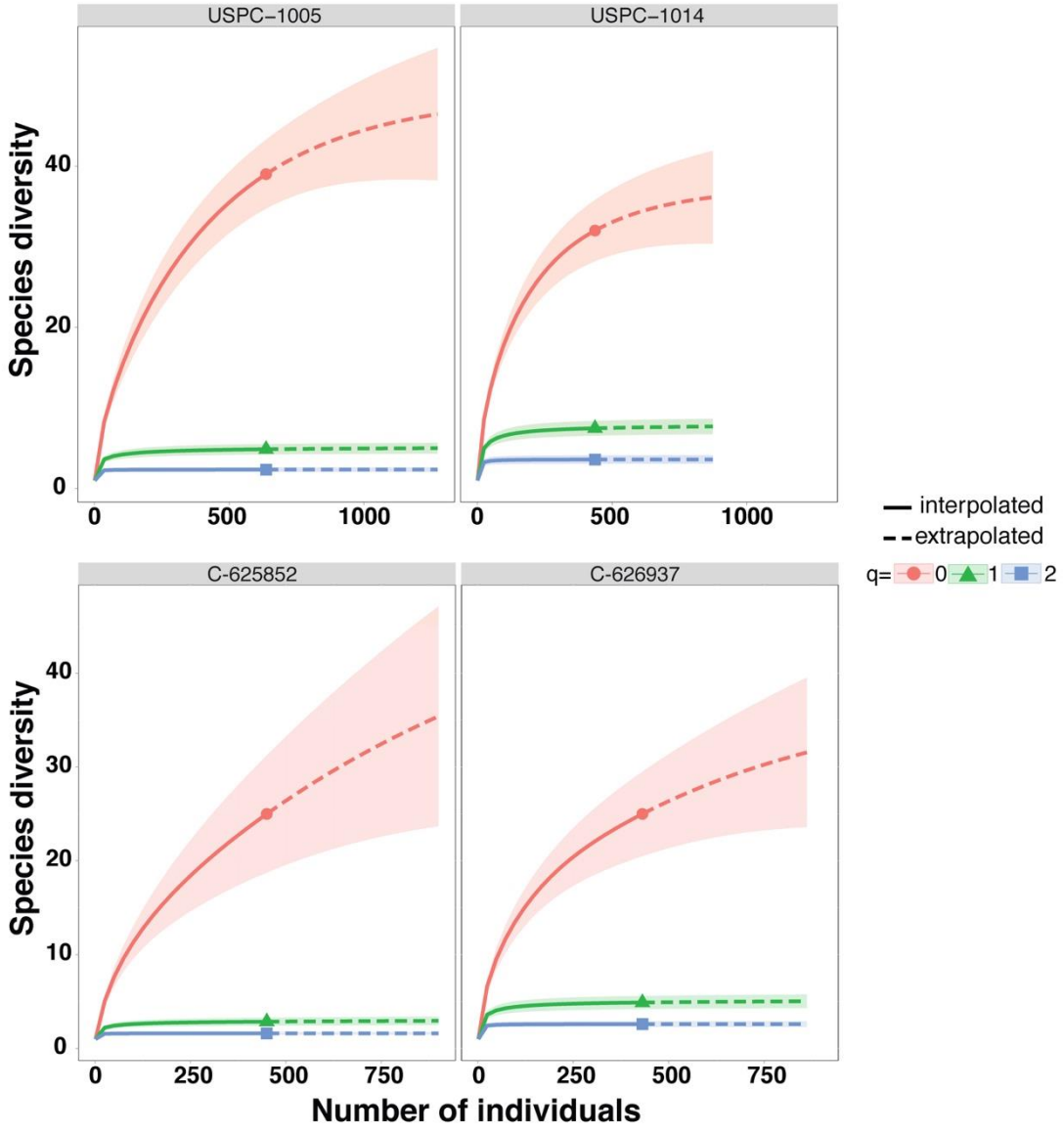

Figure S2: Shows curves for each Hill number (q = 0, 1, 2) for the pollen count data including localities USPC-1005, USPC-1014, and the stratigraphically nearby coal layers C-625852 and C-626937. The first curve (q = 0) is a classical rarefaction curve (also found in the main document). The second curve represents a rarefaction curve based on the Shannon Diversity Index (q = 1) and shows interpolated number of common species inherent to the fossil collection, the dashed line shows the extrapolated number of common species were the sample size to increase. This curve does not rise in number, suggesting that the common elements of the fossil locality have already been identified. The third curve represents a curve based on Simpsons Diversity (q = 2) and shows the interpolated number of dominant species, the dashed line shows the extrapolated number of dominant species if the sample number were to increase. Similar to that of the Shannon diversity

curve, the asymptote has already been reached and no new dominant morphotypes are predicted to be found.

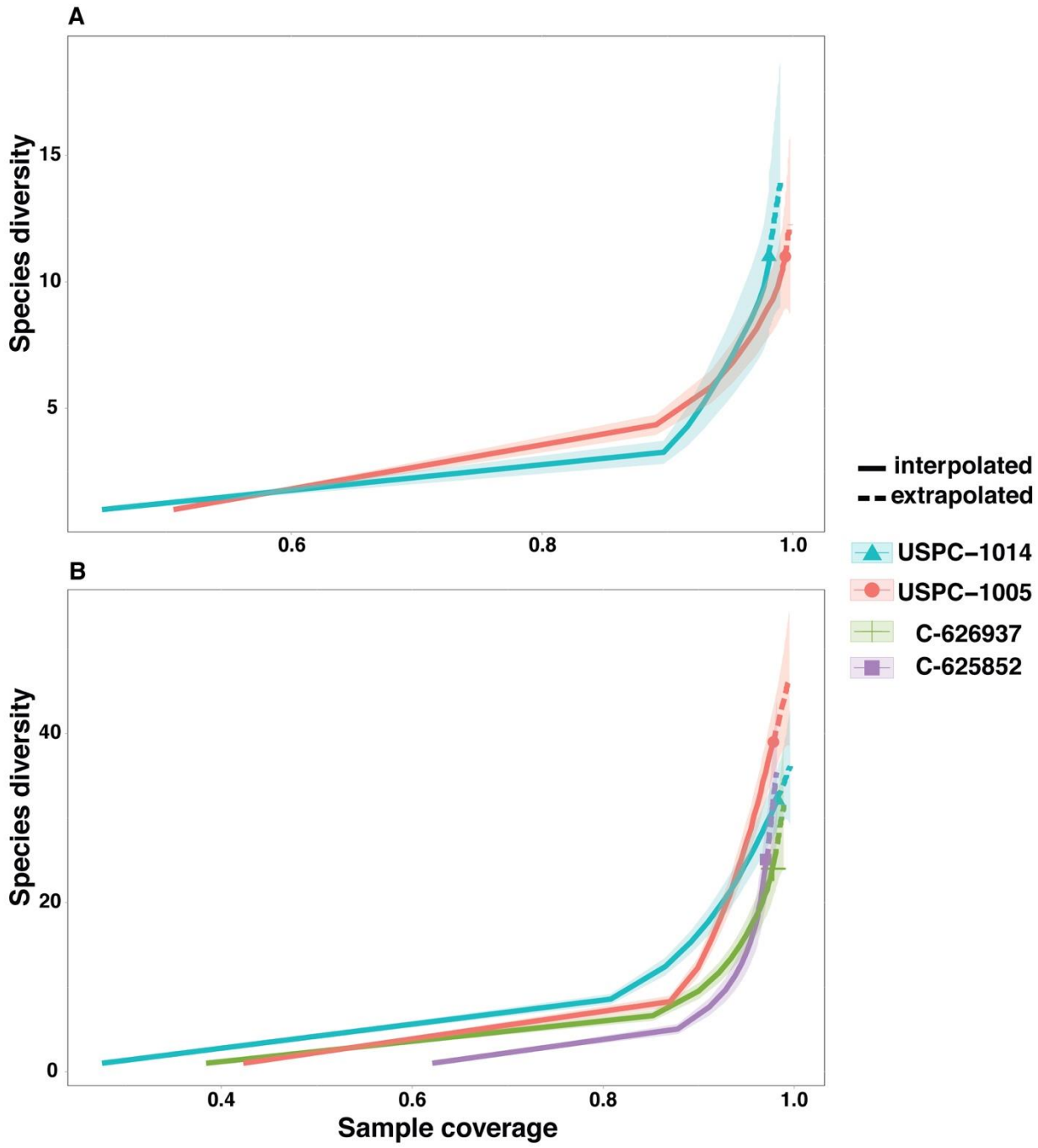

Figure S3: Coverage-based diversity estimates for (A) leaf megaflora and, (B) pollen counts from fossil localities USPC-1005 and USPC-1014, and accompanying coal layers C-625852 and C-626937.

Morphotype ID	USPC-1014	USPC-1005
Trochodendroides sp.	56	221
Vitiphyllum sp.	3	6
Archeampelos sp.	3	35
Aesculus sp.	3	28
Ushia sp.	1	9
Ulmus sp.	127	0
Corylites sp.	7	5
?Betuloid sp.	0	2
Indet. sp. 1 (Entire Margin)	4	1
Indet. sp. 2 (Cordate Ven.)	1	0
Indet. sp. 3 (Pinnate Ven.)	1	0
CAF-130	1	0
?*Platanus* sp.	0	6
Indet. sp. 4	0	3
Macginitiea sp.	0	1
Metasequoia sp.	143	36
Glyptostrobus sp.	5	5
?*Taxodium* sp.	2	1
Equisetum sp.	8	16
Total Dicot	207	317
Total Conifer & Others	158	58
Total Count	365	375

Table S1: Census data for leaf compression fossils ('dicots', conifers, and horsetails), for fossil localities USPC-1005 and USPC-1014. 'Dicot' counts were used for rarefaction analysis and diversity estimates. Morphotype ID's are based on a framework developed by West et al. 2019. Some leaves could not be identified to existing morphotypes due to preservation quality and were left unidentified, but were counted and used for rarefaction analysis.

	Sample			
Taxon	**USPC-1014**	**C-626937**	**C-625852**	**USPC-1005**
Aquilapollenites tumanganicus Bolotnikova 1973	0	0	0	3
Ericipites spp. Wodehouse 1933	0	0	0	2
Pterocaryapollenites stellatus (Potonié) Potonié 1960	0	0	2	0
Alnipollenites sp. 2	3	0	0	0
Liquidambarpollenites cf. *L. mangelsdorfianus* (Traverse) Potonié 1960	0	0	0	1
Caryapollenites imparalis Nichols & Ott 1978	2	4	9	1
Caryapollenites wyomingensis Nichols & Ott 1978	1	0	0	3
Graminidites sp.	8	7	0	1
Alnipollenites verus (Potonié) Potonié 1934	0	0	0	2
Pistillipollenites mcgregorii Rouse 1962	0	0	0	1
Sparganiaceaepollenites reticulus (Doktorowicz-Hrebnicka 1960) Krutzsch & Vanhoorne 1977	3	1	0	2
Fraxinoipollenites variabilis Stanley 1965	0	2	1	0
Tricolpites reticulatus Cookson 1947	0	0	0	2
Tricolpites anguloluminosus Anderson 1960	0	0	1	1
Alnipollenites quadrapollenites (Rouse) Srivastava 1966	0	0	1	2
Pterocaryapollenites sp. 1	0	0	0	2
cf. *Triporopollenites mullensis* (Simpson) Rouse & Srivastava 1972 (tetraporate)	0	0	1	1
Tilia vescipites Wodehouse 1933	0	0	5	11
Intratriporopollenites cf. *I. instructus* (Potonié) Thompson & Pflug 1953	0	0	1	0
Tricolpites cf. *T. sagax* Norris 1967	3	0	3	3
Tricolpites sp. 2	0	0	0	1
Tricolpites hians Stanley 1965	0	4	0	0
Echitricolpites supraechinatus Pocknall & Nichols 1996	0	1	0	0
Tricolpites ringens Ward 1986	2	0	1	1
Castaneapollenites sp.	0	0	3	0
Siltaria hanleyi (Traverse) Pocknall & Nichols 1996	0	0	1	0
Tricolporites sp. 1	0	0	1	0
Tricolpites cf. *T. parvistriatus* Norton & Hall 1967	0	0	1	0
Kurtzipites cf. *K. trispissatus* Anderson 1960	0	3	0	0
Triporopollenites mullensis (Simpson) Rouse & Srivastava 1972	44	19	8	65
Ulmipollenites tricostatus (Anderson) Farabee & Canright 1986	1	0	15	0
Alnipollenites trina (Stanley) Norton in Norton & Hall 1969	0	0	1	0
Momipites wyomingensis Nichols & Ott 1978	3	1	1	0
Paraalnipollenites alterniporus (Simpson) Srivastava 1975	0	5	1	2
Triporopollenites triplicatus (Anderson) Nichols 2002	3	5	0	6
Kurtzipites andersonii Srivastava 1981	1	0	0	0
Triporopollenites sp. 2	0	0	0	1
cf. *Pentapollenites pentangulus* Pflug 1953	3	0	0	0
Abiespollenites sp.	11	4	0	5
Pinuspollenites sp.	30	24	0	26
Piceapollenites sp.	0	2	2	0
Cathayapollenites sp.	11	64	2	3
Podocarpidites sp.	1	2	0	2

	Sample			
Taxon	**USPC-1014**	**C-626937**	**C-625852**	**USPC-1005**
Cupressacites hiatipites (Wodehouse 1933) Krutzsch 1971	217	257	353	405
Sequoiapollenites cf. *S. paleocenicus* Stanley 1965	0	0	1	1
Baculatisporites primarius (Wolff 1933) Thomson & Pflug 1953	8	0	5	5
cf. *Varirugosporites tolmanensis* Srivastava 1972	1	0	0	0
cf. *Multinodisporites* sp.	0	1	0	0
cf. *Equisetosporites* sp.	1	0	0	0
Retitriletes cf. *R. austroclavadites* (Cookson) Krutzsch 1963	4	3	0	1
Laevigatosporites haardti (Potonié & Venitz) Thomson & Pflug 1953	49	17	30	53
Hazaria sheoparii Srivastava 1971	1	0	0	2
Unidentified inaperturate spore 2	0	1	0	1
Ovoidites elongatus (Hunger) Krutzsch 1959	0	1	0	0
Leiotriletes paramaximus (Krutzsch) Krutzsch & Vanhoorne 1977	0	1	0	0
Unidentified inaperturate spore 5	2	0	0	0
Cingutriletes clavus (Balme) Dettmann 1963	0	0	0	1
Cyathidites minor Couper 1953)	2	0	0	4
Gleicheniidites senonicus Ross 1949	5	0	0	7
Cyathidites cf. *C. diaphana* (Wilson & Webster 1946) Nichols & Brown 1992	3	0	0	0
Stereigranisporis regius (Drozhastichich) Ravn & Witzke 1995	2	1	0	2
Stereisporites cf. *S. antiquasporites* Krutzsch 1963	9	1	0	4
cf. *Stereigranisporis regius* (Drozhastichich) Ravn & Witzke 1995	2	0	0	0
Biretisporites potonei Delcourt & Sprumont 1955	0	0	0	1
Unidentified inaperturate spore 3	1	0	0	0
TOTAL COUNT	437	431	450	637

Table S2: Pollen counts for fossil localities USPC-1005 and USPC-1014 and accompanying coal layers C-626937 and C-625852.

m	method	order	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
1	interpolated	0	1	1	1	0.506	0.449	0.564
18	interpolated	0	4.355	3.923	4.786	0.891	0.869	0.912
36	interpolated	0	5.863	5.162	6.564	0.935	0.921	0.95
53	interpolated	0	6.812	5.935	7.688	0.952	0.941	0.964
71	interpolated	0	7.571	6.552	8.59	0.963	0.953	0.973
88	interpolated	0	8.134	7.001	9.266	0.971	0.961	0.98
106	interpolated	0	8.61	7.372	9.849	0.976	0.968	0.985
123	interpolated	0	8.977	7.647	10.307	0.98	0.973	0.988
141	interpolated	0	9.3	7.881	10.719	0.984	0.976	0.991
158	interpolated	0	9.558	8.061	11.056	0.986	0.979	0.993
176	interpolated	0	9.794	8.219	11.37	0.988	0.981	0.994
193	interpolated	0	9.991	8.346	11.635	0.989	0.983	0.996
211	interpolated	0	10.177	8.463	11.891	0.99	0.984	0.997
228	interpolated	0	10.336	8.56	12.113	0.991	0.985	0.997
246	interpolated	0	10.491	8.65	12.331	0.992	0.986	0.998
263	interpolated	0	10.626	8.727	12.525	0.992	0.986	0.999
281	interpolated	0	10.759	8.8	12.718	0.993	0.987	0.999
298	interpolated	0	10.877	8.862	12.891	0.993	0.987	1
316	interpolated	0	10.994	8.921	13.067	0.994	0.987	1
317	observed	0	11	8.924	13.076	0.994	0.987	1.001
318	extrapolated	0	11.006	8.927	13.086	0.994	0.987	1.001
334	extrapolated	0	11.104	8.967	13.242	0.994	0.987	1.001
351	extrapolated	0	11.203	9.003	13.404	0.994	0.988	1.001
367	extrapolated	0	11.291	9.031	13.552	0.995	0.988	1.001
384	extrapolated	0	11.38	9.055	13.705	0.995	0.989	1.001
401	extrapolated	0	11.465	9.075	13.854	0.995	0.989	1.001
417	extrapolated	0	11.54	9.089	13.991	0.995	0.99	1.001
434	extrapolated	0	11.616	9.101	14.132	0.996	0.99	1.001
451	extrapolated	0	11.688	9.109	14.268	0.996	0.99	1.001
467	extrapolated	0	11.753	9.113	14.392	0.996	0.991	1.001
484	extrapolated	0	11.817	9.115	14.52	0.996	0.991	1.001
500	extrapolated	0	11.875	9.115	14.636	0.996	0.992	1.001
517	extrapolated	0	11.934	9.112	14.756	0.997	0.992	1.001
534	extrapolated	0	11.989	9.107	14.871	0.997	0.992	1.001
550	extrapolated	0	12.039	9.102	14.976	0.997	0.992	1.001
567	extrapolated	0	12.089	9.094	15.083	0.997	0.993	1.001
584	extrapolated	0	12.136	9.085	15.187	0.997	0.993	1.002
600	extrapolated	0	12.178	9.076	15.281	0.997	0.993	1.002
617	extrapolated	0	12.221	9.065	15.377	0.998	0.994	1.002
634	extrapolated	0	12.261	9.053	15.47	0.998	0.994	1.002
1	interpolated	1	1	1	1	0.506	0.437	0.576
18	interpolated	1	2.531	2.212	2.849	0.891	0.869	0.912
36	interpolated	1	2.772	2.404	3.14	0.935	0.921	0.95
53	interpolated	1	2.875	2.487	3.263	0.952	0.94	0.965
71	interpolated	1	2.939	2.539	3.34	0.963	0.952	0.975

m	method	order	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
88	interpolated	1	2.98	2.572	3.388	0.971	0.96	0.981
106	interpolated	1	3.01	2.597	3.424	0.976	0.966	0.986
123	interpolated	1	3.032	2.614	3.449	0.98	0.971	0.99
141	interpolated	1	3.049	2.629	3.47	0.984	0.975	0.992
158	interpolated	1	3.063	2.64	3.486	0.986	0.978	0.994
176	interpolated	1	3.074	2.649	3.499	0.988	0.98	0.995
193	interpolated	1	3.083	2.657	3.51	0.989	0.982	0.996
211	interpolated	1	3.091	2.663	3.519	0.99	0.983	0.997
228	interpolated	1	3.098	2.669	3.527	0.991	0.984	0.998
246	interpolated	1	3.104	2.674	3.534	0.992	0.985	0.999
263	interpolated	1	3.109	2.678	3.54	0.992	0.986	0.999
281	interpolated	1	3.114	2.681	3.546	0.993	0.986	1
298	interpolated	1	3.117	2.685	3.55	0.993	0.986	1
316	interpolated	1	3.121	2.688	3.555	0.994	0.987	1.001
317	observed	1	3.121	2.688	3.555	0.994	0.987	1.001
318	extrapolated	1	3.122	2.688	3.555	0.994	0.987	1.001
334	extrapolated	1	3.125	2.691	3.559	0.994	0.987	1.001
351	extrapolated	1	3.128	2.693	3.562	0.994	0.988	1.001
367	extrapolated	1	3.13	2.696	3.565	0.995	0.988	1.001
384	extrapolated	1	3.133	2.698	3.569	0.995	0.989	1.001
401	extrapolated	1	3.136	2.7	3.572	0.995	0.989	1.001
417	extrapolated	1	3.138	2.702	3.575	0.995	0.989	1.001
434	extrapolated	1	3.141	2.704	3.577	0.996	0.99	1.001
451	extrapolated	1	3.143	2.706	3.58	0.996	0.99	1.001
467	extrapolated	1	3.145	2.707	3.582	0.996	0.991	1.002
484	extrapolated	1	3.147	2.709	3.585	0.996	0.991	1.002
500	extrapolated	1	3.149	2.711	3.587	0.996	0.991	1.002
517	extrapolated	1	3.151	2.712	3.589	0.997	0.992	1.002
534	extrapolated	1	3.152	2.714	3.591	0.997	0.992	1.002
550	extrapolated	1	3.154	2.715	3.593	0.997	0.992	1.002
567	extrapolated	1	3.156	2.716	3.595	0.997	0.993	1.002
584	extrapolated	1	3.157	2.717	3.597	0.997	0.993	1.002
600	extrapolated	1	3.159	2.719	3.598	0.997	0.993	1.002
617	extrapolated	1	3.16	2.72	3.6	0.998	0.993	1.002
634	extrapolated	1	3.161	2.721	3.602	0.998	0.994	1.002
1	interpolated	2	1	1	1	0.506	0.443	0.57
18	interpolated	2	1.873	1.664	2.082	0.891	0.869	0.912
36	interpolated	2	1.923	1.696	2.15	0.935	0.921	0.949
53	interpolated	2	1.939	1.706	2.172	0.952	0.94	0.964
71	interpolated	2	1.948	1.712	2.184	0.963	0.952	0.974
88	interpolated	2	1.953	1.715	2.191	0.971	0.96	0.981
106	interpolated	2	1.957	1.717	2.196	0.976	0.966	0.986
123	interpolated	2	1.959	1.719	2.2	0.98	0.971	0.99
141	interpolated	2	1.961	1.72	2.202	0.984	0.975	0.992
158	interpolated	2	1.963	1.721	2.204	0.986	0.978	0.994

m	method	order	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
176	interpolated	2	1.964	1.722	2.206	0.988	0.98	0.996
193	interpolated	2	1.965	1.722	2.207	0.989	0.982	0.997
211	interpolated	2	1.966	1.723	2.208	0.99	0.983	0.998
228	interpolated	2	1.966	1.723	2.209	0.991	0.984	0.998
246	interpolated	2	1.967	1.724	2.21	0.992	0.985	0.999
263	interpolated	2	1.967	1.724	2.211	0.992	0.985	0.999
281	interpolated	2	1.968	1.724	2.212	0.993	0.986	1
298	interpolated	2	1.968	1.725	2.212	0.993	0.986	1.001
316	interpolated	2	1.969	1.725	2.213	0.994	0.986	1.001
317	observed	2	1.969	1.725	2.213	0.994	0.986	1.001
318	extrapolated	2	1.969	1.725	2.213	0.994	0.986	1.001
334	extrapolated	2	1.969	1.725	2.213	0.994	0.987	1.001
351	extrapolated	2	1.969	1.725	2.213	0.994	0.987	1.002
367	extrapolated	2	1.97	1.725	2.214	0.995	0.988	1.002
384	extrapolated	2	1.97	1.725	2.214	0.995	0.988	1.002
401	extrapolated	2	1.97	1.726	2.214	0.995	0.988	1.002
417	extrapolated	2	1.97	1.726	2.215	0.995	0.989	1.002
434	extrapolated	2	1.97	1.726	2.215	0.996	0.989	1.002
451	extrapolated	2	1.971	1.726	2.215	0.996	0.99	1.002
467	extrapolated	2	1.971	1.726	2.215	0.996	0.99	1.002
484	extrapolated	2	1.971	1.726	2.216	0.996	0.99	1.002
500	extrapolated	2	1.971	1.726	2.216	0.996	0.991	1.002
517	extrapolated	2	1.971	1.726	2.216	0.997	0.991	1.002
534	extrapolated	2	1.971	1.726	2.216	0.997	0.991	1.002
550	extrapolated	2	1.971	1.726	2.216	0.997	0.992	1.002
567	extrapolated	2	1.971	1.726	2.216	0.997	0.992	1.002
584	extrapolated	2	1.971	1.726	2.216	0.997	0.992	1.002
600	extrapolated	2	1.972	1.727	2.217	0.997	0.992	1.002
617	extrapolated	2	1.972	1.727	2.217	0.998	0.993	1.002
634	extrapolated	2	1.972	1.727	2.217	0.998	0.993	1.002

Table S3: USPC-1005 Hill number (q = 0, 1, 2) data for leaf megaflora. Dicots only. m = sample size for the diversity estimates of order q are computed; method states whether the estimate has been interpolated, extrapolated, or observed and depends on if m is less than, equal to, or greater than the sample size; order relates to the diversity order selected (q = 0, 1, 2); qD is equal to the estimate diversity of order q for the sample size of m; SC is equal to the estimated sample coverage for the sample size of m; qD.LCL & qD.UCL equal the bootstrapped lower and upper confidence limits (0.95) for the diversity order q; SC.LCL & SC.UCL equal the bootstrapped lower and upper confidence limits (0.95) for the predicted sample coverage (Hsieh et al. 2016).

m	method	order	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
1	interpolated	0	1	1	1	0.449	0.394	0.505
12	interpolated	0	3.266	2.833	3.698	0.897	0.866	0.928
23	interpolated	0	4.286	3.571	5.002	0.916	0.893	0.94
35	interpolated	0	5.219	4.269	6.169	0.929	0.909	0.949
46	interpolated	0	5.953	4.823	7.083	0.938	0.92	0.957
57	interpolated	0	6.593	5.302	7.884	0.946	0.928	0.964
69	interpolated	0	7.201	5.748	8.654	0.953	0.936	0.97
80	interpolated	0	7.69	6.098	9.281	0.958	0.942	0.974
92	interpolated	0	8.161	6.426	9.897	0.963	0.948	0.979
103	interpolated	0	8.546	6.684	10.408	0.967	0.952	0.982
114	interpolated	0	8.893	6.909	10.877	0.97	0.955	0.985
126	interpolated	0	9.236	7.122	11.349	0.973	0.958	0.988
137	interpolated	0	9.522	7.293	11.751	0.975	0.96	0.99
149	interpolated	0	9.81	7.457	12.163	0.977	0.962	0.992
160	interpolated	0	10.056	7.591	12.521	0.978	0.963	0.994
171	interpolated	0	10.289	7.712	12.865	0.979	0.964	0.995
183	interpolated	0	10.532	7.834	13.229	0.98	0.964	0.996
194	interpolated	0	10.748	7.94	13.557	0.981	0.965	0.997
206	interpolated	0	10.981	8.05	13.911	0.981	0.964	0.997
207	observed	0	11	8.059	13.941	0.981	0.964	0.997
208	extrapolated	0	11.019	8.068	13.97	0.981	0.964	0.997
218	extrapolated	0	11.208	8.153	14.264	0.981	0.965	0.998
229	extrapolated	0	11.41	8.235	14.584	0.982	0.965	0.999
240	extrapolated	0	11.604	8.306	14.901	0.983	0.966	1
251	extrapolated	0	11.791	8.368	15.215	0.983	0.966	1
262	extrapolated	0	11.972	8.419	15.525	0.984	0.967	1.001
273	extrapolated	0	12.147	8.462	15.831	0.984	0.968	1.001
283	extrapolated	0	12.3	8.494	16.106	0.985	0.968	1.002
294	extrapolated	0	12.463	8.522	16.405	0.985	0.969	1.002
305	extrapolated	0	12.621	8.542	16.699	0.986	0.97	1.002
316	extrapolated	0	12.772	8.557	16.988	0.986	0.97	1.003
327	extrapolated	0	12.919	8.566	17.273	0.987	0.971	1.003
338	extrapolated	0	13.061	8.569	17.552	0.987	0.972	1.003
348	extrapolated	0	13.185	8.568	17.802	0.988	0.972	1.003
359	extrapolated	0	13.317	8.562	18.072	0.988	0.973	1.003
370	extrapolated	0	13.445	8.553	18.337	0.989	0.974	1.004
381	extrapolated	0	13.568	8.539	18.596	0.989	0.974	1.004
392	extrapolated	0	13.687	8.523	18.851	0.989	0.975	1.004
403	extrapolated	0	13.801	8.503	19.1	0.99	0.975	1.004
414	extrapolated	0	13.912	8.48	19.344	0.99	0.976	1.004
1	interpolated	1	1	1	1	0.449	0.384	0.514
12	interpolated	1	2.415	2.104	2.726	0.897	0.865	0.928
23	interpolated	1	2.64	2.248	3.031	0.916	0.893	0.939
35	interpolated	1	2.763	2.327	3.2	0.929	0.91	0.948
46	interpolated	1	2.835	2.373	3.298	0.938	0.921	0.955

m	method	order	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
57	interpolated	1	2.887	2.406	3.368	0.946	0.93	0.962
69	interpolated	1	2.929	2.434	3.424	0.953	0.938	0.968
80	interpolated	1	2.959	2.453	3.465	0.958	0.944	0.973
92	interpolated	1	2.985	2.471	3.5	0.963	0.95	0.977
103	interpolated	1	3.005	2.484	3.526	0.967	0.954	0.98
114	interpolated	1	3.021	2.495	3.548	0.97	0.957	0.983
126	interpolated	1	3.037	2.505	3.569	0.973	0.961	0.985
137	interpolated	1	3.049	2.513	3.585	0.975	0.963	0.987
149	interpolated	1	3.06	2.521	3.6	0.977	0.965	0.989
160	interpolated	1	3.07	2.527	3.612	0.978	0.967	0.99
171	interpolated	1	3.078	2.532	3.624	0.979	0.968	0.991
183	interpolated	1	3.086	2.538	3.634	0.98	0.969	0.991
194	interpolated	1	3.093	2.542	3.643	0.981	0.97	0.992
206	interpolated	1	3.099	2.546	3.652	0.981	0.97	0.992
207	observed	1	3.1	2.547	3.653	0.981	0.97	0.992
208	extrapolated	1	3.1	2.547	3.653	0.981	0.97	0.992
218	extrapolated	1	3.105	2.551	3.66	0.981	0.97	0.993
229	extrapolated	1	3.111	2.554	3.667	0.982	0.971	0.993
240	extrapolated	1	3.116	2.558	3.674	0.983	0.971	0.994
251	extrapolated	1	3.121	2.561	3.681	0.983	0.972	0.995
262	extrapolated	1	3.126	2.565	3.687	0.984	0.972	0.995
273	extrapolated	1	3.131	2.568	3.693	0.984	0.973	0.996
283	extrapolated	1	3.135	2.57	3.699	0.985	0.974	0.996
294	extrapolated	1	3.139	2.573	3.704	0.985	0.974	0.997
305	extrapolated	1	3.143	2.576	3.71	0.986	0.975	0.997
316	extrapolated	1	3.147	2.579	3.715	0.986	0.975	0.998
327	extrapolated	1	3.151	2.582	3.72	0.987	0.976	0.998
338	extrapolated	1	3.154	2.584	3.724	0.987	0.977	0.998
348	extrapolated	1	3.157	2.586	3.728	0.988	0.977	0.998
359	extrapolated	1	3.161	2.589	3.733	0.988	0.978	0.999
370	extrapolated	1	3.164	2.591	3.737	0.989	0.978	0.999
381	extrapolated	1	3.167	2.593	3.741	0.989	0.979	0.999
392	extrapolated	1	3.17	2.595	3.745	0.989	0.98	0.999
403	extrapolated	1	3.173	2.597	3.748	0.99	0.98	0.999
414	extrapolated	1	3.175	2.599	3.752	0.99	0.981	1
1	interpolated	2	1	1	1	0.449	0.382	0.516
12	interpolated	2	2.02	1.779	2.261	0.897	0.863	0.93
23	interpolated	2	2.114	1.838	2.389	0.916	0.891	0.942
35	interpolated	2	2.151	1.862	2.44	0.929	0.908	0.95
46	interpolated	2	2.168	1.873	2.464	0.938	0.919	0.957
57	interpolated	2	2.179	1.879	2.479	0.946	0.928	0.964
69	interpolated	2	2.187	1.884	2.491	0.953	0.936	0.97
80	interpolated	2	2.193	1.887	2.498	0.958	0.942	0.975
92	interpolated	2	2.197	1.89	2.504	0.963	0.947	0.979
103	interpolated	2	2.2	1.892	2.508	0.967	0.951	0.983

m	method	order	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
114	interpolated	2	2.203	1.893	2.512	0.97	0.954	0.986
126	interpolated	2	2.205	1.895	2.515	0.973	0.958	0.988
137	interpolated	2	2.207	1.896	2.517	0.975	0.96	0.99
149	interpolated	2	2.208	1.897	2.519	0.977	0.962	0.992
160	interpolated	2	2.209	1.898	2.521	0.978	0.964	0.993
171	interpolated	2	2.21	1.898	2.523	0.979	0.965	0.994
183	interpolated	2	2.211	1.899	2.524	0.98	0.966	0.994
194	interpolated	2	2.212	1.899	2.525	0.981	0.966	0.995
206	interpolated	2	2.213	1.9	2.526	0.981	0.967	0.995
207	observed	2	2.213	1.9	2.526	0.981	0.966	0.995
208	extrapolated	2	2.213	1.9	2.527	0.981	0.966	0.995
218	extrapolated	2	2.214	1.9	2.527	0.981	0.967	0.996
229	extrapolated	2	2.214	1.901	2.528	0.982	0.968	0.996
240	extrapolated	2	2.215	1.901	2.529	0.983	0.968	0.997
251	extrapolated	2	2.215	1.901	2.53	0.983	0.969	0.997
262	extrapolated	2	2.216	1.902	2.53	0.984	0.97	0.998
273	extrapolated	2	2.216	1.902	2.531	0.984	0.97	0.998
283	extrapolated	2	2.217	1.902	2.531	0.985	0.971	0.999
294	extrapolated	2	2.217	1.902	2.532	0.985	0.972	0.999
305	extrapolated	2	2.217	1.902	2.532	0.986	0.972	1
316	extrapolated	2	2.218	1.903	2.533	0.986	0.973	1
327	extrapolated	2	2.218	1.903	2.533	0.987	0.974	1
338	extrapolated	2	2.218	1.903	2.534	0.987	0.974	1
348	extrapolated	2	2.218	1.903	2.534	0.988	0.975	1.001
359	extrapolated	2	2.219	1.903	2.534	0.988	0.975	1.001
370	extrapolated	2	2.219	1.903	2.534	0.989	0.976	1.001
381	extrapolated	2	2.219	1.903	2.535	0.989	0.977	1.001
392	extrapolated	2	2.219	1.904	2.535	0.989	0.977	1.002
403	extrapolated	2	2.22	1.904	2.535	0.99	0.978	1.002
414	extrapolated	2	2.22	1.904	2.536	0.99	0.978	1.002

Table S4: USPC-1014 Hill number (q = 0, 1, 2) data for leaf macroflora. Dicots only. m = sample size for the diversity estimates of order q are computed; method states whether the estimate has been interpolated, extrapolated, or observed and depends on if m is less than, equal to, or greater than the sample size; order relates to the diversity order selected (q = 0, 1, 2); qD is equal to the estimate diversity of order q for the sample size of m; SC is equal to the estimated sample coverage for the sample size of m; qD.LCL & qD.UCL equal the bootstrapped lower and upper confidence limits (0.95) for the diversity order q; SC.LCL & SC.UCL equal the bootstrapped lower and upper confidence limits (0.95) for the predicted sample coverage (Hsieh et al. 2016).

m	method	order	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
1	interpolated	0	1	1	1	0.423	0.386	0.46
36	interpolated	0	8.289	7.509	9.069	0.87	0.851	0.889
71	interpolated	0	12.271	10.971	13.571	0.899	0.885	0.912
106	interpolated	0	15.549	13.867	17.231	0.913	0.902	0.925
142	interpolated	0	18.469	16.473	20.465	0.924	0.914	0.934
177	interpolated	0	20.974	18.72	23.228	0.933	0.923	0.942
212	interpolated	0	23.213	20.734	25.693	0.939	0.931	0.948
247	interpolated	0	25.231	22.549	27.913	0.945	0.937	0.954
283	interpolated	0	27.111	24.239	29.984	0.95	0.942	0.958
318	interpolated	0	28.775	25.73	31.82	0.955	0.947	0.963
353	interpolated	0	30.298	27.092	33.505	0.958	0.951	0.966
389	interpolated	0	31.736	28.37	35.101	0.962	0.954	0.969
424	interpolated	0	33.022	29.507	36.536	0.965	0.957	0.972
459	interpolated	0	34.208	30.549	37.868	0.967	0.96	0.975
494	interpolated	0	35.305	31.503	39.107	0.97	0.962	0.977
530	interpolated	0	36.348	32.401	40.295	0.972	0.965	0.98
565	interpolated	0	37.286	33.197	41.374	0.974	0.967	0.982
600	interpolated	0	38.153	33.921	42.385	0.976	0.969	0.984
636	interpolated	0	38.978	34.596	43.36	0.978	0.97	0.986
637	observed	0	39	34.614	43.386	0.978	0.97	0.986
638	extrapolated	0	39.022	34.632	43.412	0.978	0.971	0.986
671	extrapolated	0	39.719	35.187	44.25	0.98	0.972	0.987
704	extrapolated	0	40.366	35.689	45.042	0.981	0.973	0.989
738	extrapolated	0	40.984	36.154	45.814	0.983	0.975	0.99
771	extrapolated	0	41.541	36.558	46.523	0.984	0.976	0.992
805	extrapolated	0	42.073	36.93	47.215	0.985	0.977	0.993
838	extrapolated	0	42.552	37.251	47.853	0.986	0.978	0.994
872	extrapolated	0	43.01	37.542	48.477	0.987	0.979	0.995
905	extrapolated	0	43.422	37.792	49.052	0.988	0.98	0.996
939	extrapolated	0	43.816	38.016	49.615	0.989	0.981	0.996
972	extrapolated	0	44.17	38.205	50.135	0.99	0.982	0.997
1006	extrapolated	0	44.509	38.373	50.645	0.99	0.983	0.998
1039	extrapolated	0	44.814	38.513	51.116	0.991	0.984	0.998
1073	extrapolated	0	45.106	38.634	51.578	0.992	0.985	0.999
1106	extrapolated	0	45.368	38.732	52.005	0.992	0.985	0.999
1140	extrapolated	0	45.619	38.815	52.424	0.993	0.986	1
1173	extrapolated	0	45.845	38.879	52.811	0.993	0.987	1
1207	extrapolated	0	46.061	38.931	53.191	0.994	0.987	1.001
1240	extrapolated	0	46.255	38.968	53.543	0.994	0.988	1.001
1274	extrapolated	0	46.441	38.994	53.889	0.995	0.988	1.001
1	interpolated	1	1	1	1	0.423	0.387	0.46
36	interpolated	1	3.637	3.267	4.007	0.87	0.85	0.889
71	interpolated	1	4.036	3.581	4.491	0.899	0.885	0.913
106	interpolated	1	4.243	3.744	4.743	0.913	0.902	0.925
142	interpolated	1	4.381	3.852	4.909	0.924	0.914	0.934

m	method	order	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
177	interpolated	1	4.477	3.928	5.025	0.933	0.923	0.942
212	interpolated	1	4.549	3.987	5.112	0.939	0.931	0.948
247	interpolated	1	4.607	4.033	5.181	0.945	0.937	0.953
283	interpolated	1	4.656	4.072	5.239	0.95	0.942	0.958
318	interpolated	1	4.695	4.104	5.285	0.955	0.947	0.962
353	interpolated	1	4.728	4.131	5.325	0.958	0.951	0.966
389	interpolated	1	4.757	4.155	5.359	0.962	0.954	0.969
424	interpolated	1	4.782	4.176	5.388	0.965	0.957	0.973
459	interpolated	1	4.803	4.193	5.413	0.967	0.96	0.975
494	interpolated	1	4.822	4.209	5.435	0.97	0.962	0.978
530	interpolated	1	4.84	4.224	5.456	0.972	0.964	0.98
565	interpolated	1	4.855	4.236	5.473	0.974	0.966	0.983
600	interpolated	1	4.869	4.248	5.489	0.976	0.967	0.985
636	interpolated	1	4.881	4.258	5.504	0.978	0.969	0.987
637	observed	1	4.882	4.259	5.504	0.978	0.969	0.987
638	extrapolated	1	4.882	4.259	5.505	0.978	0.969	0.987
671	extrapolated	1	4.893	4.268	5.517	0.98	0.97	0.989
704	extrapolated	1	4.903	4.277	5.529	0.981	0.972	0.991
738	extrapolated	1	4.913	4.285	5.54	0.983	0.973	0.992
771	extrapolated	1	4.922	4.293	5.551	0.984	0.974	0.994
805	extrapolated	1	4.931	4.3	5.561	0.985	0.975	0.995
838	extrapolated	1	4.939	4.307	5.571	0.986	0.976	0.996
872	extrapolated	1	4.947	4.314	5.58	0.987	0.977	0.997
905	extrapolated	1	4.954	4.32	5.589	0.988	0.978	0.998
939	extrapolated	1	4.962	4.326	5.597	0.989	0.979	0.999
972	extrapolated	1	4.968	4.332	5.605	0.99	0.98	1
1006	extrapolated	1	4.975	4.337	5.613	0.99	0.981	1
1039	extrapolated	1	4.981	4.342	5.62	0.991	0.981	1.001
1073	extrapolated	1	4.987	4.347	5.626	0.992	0.982	1.001
1106	extrapolated	1	4.992	4.351	5.633	0.992	0.983	1.002
1140	extrapolated	1	4.997	4.356	5.639	0.993	0.983	1.002
1173	extrapolated	1	5.002	4.36	5.645	0.993	0.984	1.003
1207	extrapolated	1	5.007	4.364	5.65	0.994	0.985	1.003
1240	extrapolated	1	5.011	4.368	5.655	0.994	0.985	1.004
1274	extrapolated	1	5.016	4.371	5.66	0.995	0.986	1.004
1	interpolated	2	1	1	1	0.423	0.377	0.469
36	interpolated	2	2.276	2.044	2.509	0.87	0.848	0.892
71	interpolated	2	2.318	2.074	2.562	0.899	0.882	0.916
106	interpolated	2	2.333	2.084	2.581	0.913	0.899	0.928
142	interpolated	2	2.34	2.09	2.591	0.924	0.912	0.937
177	interpolated	2	2.345	2.093	2.596	0.933	0.921	0.944
212	interpolated	2	2.348	2.095	2.6	0.939	0.929	0.95
247	interpolated	2	2.35	2.096	2.603	0.945	0.936	0.955
283	interpolated	2	2.351	2.097	2.605	0.95	0.941	0.959
318	interpolated	2	2.353	2.098	2.607	0.955	0.946	0.963

m	method	order	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
353	interpolated	2	2.354	2.099	2.608	0.958	0.95	0.967
389	interpolated	2	2.354	2.1	2.609	0.962	0.954	0.97
424	interpolated	2	2.355	2.1	2.61	0.965	0.957	0.973
459	interpolated	2	2.356	2.1	2.611	0.967	0.959	0.976
494	interpolated	2	2.356	2.101	2.611	0.97	0.962	0.978
530	interpolated	2	2.357	2.101	2.612	0.972	0.964	0.98
565	interpolated	2	2.357	2.101	2.612	0.974	0.966	0.983
600	interpolated	2	2.357	2.102	2.613	0.976	0.968	0.985
636	interpolated	2	2.358	2.102	2.613	0.978	0.969	0.987
637	observed	2	2.358	2.102	2.613	0.978	0.969	0.987
638	extrapolated	2	2.358	2.102	2.613	0.978	0.969	0.987
671	extrapolated	2	2.358	2.102	2.614	0.98	0.97	0.989
704	extrapolated	2	2.358	2.102	2.614	0.981	0.972	0.991
738	extrapolated	2	2.358	2.102	2.614	0.983	0.973	0.992
771	extrapolated	2	2.358	2.102	2.614	0.984	0.974	0.993
805	extrapolated	2	2.359	2.103	2.615	0.985	0.975	0.995
838	extrapolated	2	2.359	2.103	2.615	0.986	0.976	0.996
872	extrapolated	2	2.359	2.103	2.615	0.987	0.977	0.997
905	extrapolated	2	2.359	2.103	2.615	0.988	0.978	0.998
939	extrapolated	2	2.359	2.103	2.615	0.989	0.979	0.999
972	extrapolated	2	2.359	2.103	2.616	0.99	0.98	0.999
1006	extrapolated	2	2.359	2.103	2.616	0.99	0.981	1
1039	extrapolated	2	2.36	2.103	2.616	0.991	0.982	1
1073	extrapolated	2	2.36	2.103	2.616	0.992	0.983	1.001
1106	extrapolated	2	2.36	2.103	2.616	0.992	0.983	1.001
1140	extrapolated	2	2.36	2.103	2.616	0.993	0.984	1.002
1173	extrapolated	2	2.36	2.103	2.616	0.993	0.985	1.002
1207	extrapolated	2	2.36	2.104	2.616	0.994	0.985	1.002
1240	extrapolated	2	2.36	2.104	2.616	0.994	0.986	1.003
1274	extrapolated	2	2.36	2.104	2.617	0.995	0.987	1.003

Table S5: USPC-1005 Hill number (q = 0, 1, 2) data for pollen counts. m = sample size for the diversity estimates of order q are computed; method states whether the estimate has been interpolated, extrapolated, or observed and depends on if m is less than, equal to, or greater than the sample size; order relates to the diversity order selected (q = 0, 1, 2); qD is equal to the estimate diversity of order q for the sample size of m; SC is equal to the estimated sample coverage for the sample size of m; qD.LCL & qD.UCL equal the bootstrapped lower and upper confidence limits (0.95) for the diversity order q; SC.LCL & SC.UCL equal the bootstrapped lower and upper confidence limits (0.95) for the predicted sample coverage (Hsieh et al. 2016).

m	method	order	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
1	interpolated	0	1	1	1	0.621	0.558	0.684
25	interpolated	0	5.048	4.414	5.682	0.878	0.858	0.898
50	interpolated	0	7.643	6.617	8.669	0.911	0.894	0.929
75	interpolated	0	9.643	8.266	11.019	0.928	0.912	0.944
100	interpolated	0	11.315	9.608	13.022	0.938	0.923	0.953
125	interpolated	0	12.775	10.751	14.8	0.945	0.931	0.96
150	interpolated	0	14.086	11.756	16.416	0.95	0.936	0.964
175	interpolated	0	15.284	12.658	17.91	0.954	0.941	0.968
200	interpolated	0	16.395	13.482	19.308	0.957	0.944	0.97
225	interpolated	0	17.437	14.246	20.627	0.96	0.947	0.972
249	interpolated	0	18.383	14.934	21.832	0.962	0.949	0.974
274	interpolated	0	19.321	15.609	23.034	0.963	0.951	0.976
299	interpolated	0	20.219	16.25	24.187	0.965	0.953	0.977
324	interpolated	0	21.08	16.861	25.299	0.966	0.954	0.978
349	interpolated	0	21.909	17.444	26.374	0.967	0.955	0.98
374	interpolated	0	22.71	18.003	27.417	0.968	0.956	0.981
399	interpolated	0	23.486	18.54	28.432	0.969	0.957	0.982
424	interpolated	0	24.239	19.056	29.422	0.97	0.958	0.983
449	interpolated	0	24.971	19.552	30.39	0.971	0.959	0.984
450	observed	0	25	19.571	30.429	0.971	0.959	0.984
451	extrapolated	0	25.029	19.591	30.467	0.971	0.959	0.984
474	extrapolated	0	25.685	20.03	31.339	0.972	0.959	0.985
498	extrapolated	0	26.352	20.471	32.234	0.973	0.96	0.985
521	extrapolated	0	26.977	20.877	33.077	0.973	0.96	0.986
545	extrapolated	0	27.613	21.283	33.944	0.974	0.961	0.987
569	extrapolated	0	28.234	21.672	34.797	0.974	0.961	0.988
592	extrapolated	0	28.815	22.028	35.602	0.975	0.962	0.988
616	extrapolated	0	29.407	22.382	36.431	0.976	0.962	0.989
640	extrapolated	0	29.984	22.72	37.248	0.976	0.963	0.99
663	extrapolated	0	30.524	23.027	38.02	0.977	0.963	0.991
687	extrapolated	0	31.074	23.332	38.816	0.977	0.964	0.991
710	extrapolated	0	31.588	23.608	39.568	0.978	0.964	0.992
734	extrapolated	0	32.112	23.881	40.343	0.978	0.965	0.992
758	extrapolated	0	32.624	24.139	41.108	0.979	0.965	0.993
781	extrapolated	0	33.102	24.373	41.831	0.979	0.965	0.993
805	extrapolated	0	33.589	24.602	42.576	0.98	0.966	0.994
829	extrapolated	0	34.064	24.817	43.311	0.98	0.966	0.994
852	extrapolated	0	34.509	25.011	44.007	0.981	0.967	0.995
876	extrapolated	0	34.962	25.201	44.723	0.981	0.967	0.995
900	extrapolated	0	35.404	25.378	45.43	0.982	0.968	0.996
1	interpolated	1	1	1	1	0.621	0.557	0.685
25	interpolated	1	2.216	1.917	2.514	0.878	0.858	0.898
50	interpolated	1	2.428	2.074	2.783	0.911	0.894	0.928
75	interpolated	1	2.536	2.152	2.919	0.928	0.912	0.944
100	interpolated	1	2.603	2.202	3.005	0.938	0.923	0.953

m	method	order	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
125	interpolated	1	2.651	2.237	3.066	0.945	0.931	0.959
150	interpolated	1	2.688	2.263	3.112	0.95	0.936	0.964
175	interpolated	1	2.716	2.284	3.148	0.954	0.941	0.968
200	interpolated	1	2.74	2.301	3.178	0.957	0.944	0.97
225	interpolated	1	2.759	2.315	3.203	0.96	0.947	0.973
249	interpolated	1	2.775	2.327	3.224	0.962	0.949	0.974
274	interpolated	1	2.79	2.337	3.243	0.963	0.951	0.976
299	interpolated	1	2.803	2.347	3.259	0.965	0.952	0.978
324	interpolated	1	2.814	2.355	3.274	0.966	0.954	0.979
349	interpolated	1	2.824	2.362	3.287	0.967	0.955	0.98
374	interpolated	1	2.834	2.369	3.298	0.968	0.956	0.981
399	interpolated	1	2.842	2.375	3.309	0.969	0.957	0.982
424	interpolated	1	2.85	2.38	3.319	0.97	0.957	0.983
449	interpolated	1	2.857	2.385	3.328	0.971	0.958	0.984
450	observed	1	2.857	2.385	3.328	0.971	0.958	0.984
451	extrapolated	1	2.857	2.386	3.329	0.971	0.958	0.984
474	extrapolated	1	2.863	2.39	3.337	0.972	0.958	0.985
498	extrapolated	1	2.869	2.394	3.344	0.973	0.959	0.986
521	extrapolated	1	2.875	2.398	3.352	0.973	0.959	0.987
545	extrapolated	1	2.881	2.402	3.359	0.974	0.96	0.988
569	extrapolated	1	2.886	2.406	3.366	0.974	0.96	0.989
592	extrapolated	1	2.891	2.41	3.373	0.975	0.961	0.989
616	extrapolated	1	2.896	2.413	3.379	0.976	0.961	0.99
640	extrapolated	1	2.901	2.417	3.385	0.976	0.962	0.991
663	extrapolated	1	2.906	2.42	3.391	0.977	0.962	0.991
687	extrapolated	1	2.91	2.423	3.397	0.977	0.963	0.992
710	extrapolated	1	2.914	2.426	3.402	0.978	0.963	0.993
734	extrapolated	1	2.918	2.429	3.408	0.978	0.964	0.993
758	extrapolated	1	2.922	2.432	3.413	0.979	0.964	0.994
781	extrapolated	1	2.926	2.435	3.418	0.979	0.964	0.995
805	extrapolated	1	2.93	2.437	3.423	0.98	0.965	0.995
829	extrapolated	1	2.934	2.44	3.427	0.98	0.965	0.996
852	extrapolated	1	2.937	2.442	3.432	0.981	0.966	0.996
876	extrapolated	1	2.94	2.444	3.436	0.981	0.966	0.997
900	extrapolated	1	2.943	2.446	3.44	0.982	0.967	0.997
1	interpolated	2	1	1	1	0.621	0.557	0.685
25	interpolated	2	1.571	1.419	1.724	0.878	0.858	0.898
50	interpolated	2	1.59	1.431	1.749	0.911	0.895	0.927
75	interpolated	2	1.597	1.435	1.758	0.928	0.914	0.942
100	interpolated	2	1.6	1.437	1.763	0.938	0.925	0.951
125	interpolated	2	1.602	1.438	1.765	0.945	0.933	0.957
150	interpolated	2	1.603	1.439	1.767	0.95	0.938	0.962
175	interpolated	2	1.604	1.44	1.768	0.954	0.943	0.965
200	interpolated	2	1.605	1.44	1.769	0.957	0.946	0.968
225	interpolated	2	1.605	1.44	1.77	0.96	0.949	0.97

m	method	order	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
249	interpolated	2	1.606	1.441	1.771	0.962	0.952	0.972
274	interpolated	2	1.606	1.441	1.771	0.963	0.953	0.973
299	interpolated	2	1.606	1.441	1.772	0.965	0.955	0.975
324	interpolated	2	1.607	1.441	1.772	0.966	0.956	0.976
349	interpolated	2	1.607	1.441	1.772	0.967	0.958	0.977
374	interpolated	2	1.607	1.442	1.773	0.968	0.958	0.979
399	interpolated	2	1.607	1.442	1.773	0.969	0.959	0.98
424	interpolated	2	1.607	1.442	1.773	0.97	0.96	0.981
449	interpolated	2	1.607	1.442	1.773	0.971	0.96	0.982
450	observed	2	1.608	1.442	1.773	0.971	0.96	0.982
451	extrapolated	2	1.608	1.442	1.773	0.971	0.96	0.982
474	extrapolated	2	1.608	1.442	1.773	0.972	0.96	0.984
498	extrapolated	2	1.608	1.442	1.773	0.973	0.96	0.985
521	extrapolated	2	1.608	1.442	1.774	0.973	0.961	0.986
545	extrapolated	2	1.608	1.442	1.774	0.974	0.961	0.987
569	extrapolated	2	1.608	1.442	1.774	0.974	0.961	0.988
592	extrapolated	2	1.608	1.442	1.774	0.975	0.962	0.989
616	extrapolated	2	1.608	1.442	1.774	0.976	0.962	0.989
640	extrapolated	2	1.608	1.442	1.774	0.976	0.962	0.99
663	extrapolated	2	1.608	1.442	1.774	0.977	0.963	0.991
687	extrapolated	2	1.608	1.442	1.774	0.977	0.963	0.992
710	extrapolated	2	1.608	1.442	1.774	0.978	0.963	0.992
734	extrapolated	2	1.608	1.442	1.774	0.978	0.964	0.993
758	extrapolated	2	1.608	1.442	1.774	0.979	0.964	0.994
781	extrapolated	2	1.608	1.442	1.774	0.979	0.964	0.994
805	extrapolated	2	1.608	1.442	1.774	0.98	0.965	0.995
829	extrapolated	2	1.608	1.442	1.775	0.98	0.965	0.996
852	extrapolated	2	1.609	1.442	1.775	0.981	0.966	0.996
876	extrapolated	2	1.609	1.442	1.775	0.981	0.966	0.997
900	extrapolated	2	1.609	1.443	1.775	0.982	0.966	0.997

Table S6: C-625852 Hill number (q = 0, 1, 2) data for pollen count. m = sample size for the diversity estimates of order q are computed; method states whether the estimate has been interpolated, extrapolated, or observed and depends on if m is less than, equal to, or greater than the sample size; order relates to the diversity order selected (q = 0, 1, 2); qD is equal to the estimate diversity of order q for the sample size of m; SC is equal to the estimated sample coverage for the sample size of m; qD.LCL & qD.UCL equal the bootstrapped lower and upper confidence limits (0.95) for the diversity order q; SC.LCL & SC.UCL equal the bootstrapped lower and upper confidence limits (0.95) for the predicted sample coverage (Hsieh et al. 2016).

m	method	order	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
1	interpolated	0	1	1	1	0.275	0.228	0.323
25	interpolated	0	8.589	7.775	9.404	0.808	0.782	0.833
49	interpolated	0	12.435	11.174	13.695	0.865	0.848	0.882
73	interpolated	0	15.345	13.789	16.9	0.892	0.877	0.907
97	interpolated	0	17.72	15.922	19.517	0.91	0.896	0.924
121	interpolated	0	19.721	17.701	21.74	0.923	0.91	0.936
146	interpolated	0	21.51	19.273	23.747	0.934	0.922	0.946
170	interpolated	0	23.007	20.575	25.44	0.942	0.93	0.953
194	interpolated	0	24.331	21.716	26.946	0.948	0.937	0.959
218	interpolated	0	25.509	22.725	28.293	0.954	0.944	0.964
242	interpolated	0	26.562	23.623	29.502	0.959	0.949	0.968
266	interpolated	0	27.506	24.424	30.588	0.963	0.953	0.972
291	interpolated	0	28.387	25.168	31.606	0.967	0.957	0.976
315	interpolated	0	29.145	25.805	32.484	0.97	0.961	0.979
339	interpolated	0	29.827	26.375	33.278	0.973	0.964	0.982
363	interpolated	0	30.441	26.887	33.996	0.976	0.966	0.985
387	interpolated	0	30.997	27.346	34.648	0.978	0.968	0.988
411	interpolated	0	31.502	27.76	35.244	0.98	0.97	0.99
436	interpolated	0	31.982	28.148	35.815	0.982	0.972	0.992
437	observed	0	32	28.163	35.837	0.982	0.972	0.992
438	extrapolated	0	32.018	28.178	35.859	0.982	0.972	0.992
460	extrapolated	0	32.404	28.485	36.323	0.983	0.973	0.994
483	extrapolated	0	32.778	28.775	36.781	0.984	0.974	0.995
506	extrapolated	0	33.123	29.032	37.213	0.986	0.975	0.996
529	extrapolated	0	33.442	29.259	37.624	0.987	0.976	0.998
552	extrapolated	0	33.736	29.456	38.016	0.988	0.977	0.999
575	extrapolated	0	34.009	29.625	38.392	0.989	0.978	1
598	extrapolated	0	34.26	29.767	38.754	0.99	0.979	1.001
621	extrapolated	0	34.493	29.884	39.101	0.99	0.979	1.001
644	extrapolated	0	34.707	29.978	39.437	0.991	0.98	1.002
667	extrapolated	0	34.906	30.052	39.76	0.992	0.981	1.002
690	extrapolated	0	35.089	30.106	40.073	0.992	0.982	1.003
713	extrapolated	0	35.259	30.143	40.375	0.993	0.982	1.003
736	extrapolated	0	35.416	30.164	40.667	0.993	0.983	1.004
759	extrapolated	0	35.56	30.171	40.95	0.994	0.984	1.004
782	extrapolated	0	35.694	30.165	41.223	0.994	0.984	1.004
805	extrapolated	0	35.818	30.147	41.488	0.995	0.985	1.005
828	extrapolated	0	35.932	30.12	41.744	0.995	0.986	1.005
851	extrapolated	0	36.037	30.083	41.992	0.996	0.986	1.005
874	extrapolated	0	36.135	30.038	42.231	0.996	0.987	1.005
1	interpolated	1	1	1	1	0.275	0.235	0.316
25	interpolated	1	5.025	4.475	5.575	0.808	0.781	0.834
49	interpolated	1	5.851	5.145	6.558	0.865	0.843	0.886
73	interpolated	1	6.276	5.486	7.066	0.892	0.874	0.91
97	interpolated	1	6.546	5.703	7.389	0.91	0.894	0.926

m	method	order	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
121	interpolated	1	6.736	5.855	7.616	0.923	0.909	0.937
146	interpolated	1	6.883	5.974	7.791	0.934	0.921	0.946
170	interpolated	1	6.992	6.062	7.922	0.942	0.93	0.953
194	interpolated	1	7.08	6.134	8.026	0.948	0.937	0.959
218	interpolated	1	7.152	6.193	8.111	0.954	0.943	0.965
242	interpolated	1	7.213	6.242	8.183	0.959	0.948	0.969
266	interpolated	1	7.264	6.285	8.243	0.963	0.953	0.973
291	interpolated	1	7.31	6.323	8.297	0.967	0.957	0.977
315	interpolated	1	7.348	6.354	8.342	0.97	0.96	0.98
339	interpolated	1	7.381	6.382	8.381	0.973	0.963	0.983
363	interpolated	1	7.41	6.406	8.415	0.976	0.966	0.986
387	interpolated	1	7.436	6.428	8.445	0.978	0.968	0.988
411	interpolated	1	7.46	6.447	8.472	0.98	0.97	0.99
436	interpolated	1	7.481	6.466	8.497	0.982	0.971	0.992
437	observed	1	7.482	6.466	8.498	0.982	0.971	0.992
438	extrapolated	1	7.483	6.467	8.499	0.982	0.971	0.992
460	extrapolated	1	7.5	6.482	8.519	0.983	0.973	0.994
483	extrapolated	1	7.518	6.496	8.539	0.984	0.974	0.995
506	extrapolated	1	7.534	6.51	8.558	0.986	0.975	0.997
529	extrapolated	1	7.55	6.523	8.576	0.987	0.976	0.998
552	extrapolated	1	7.565	6.536	8.593	0.988	0.977	0.999
575	extrapolated	1	7.579	6.548	8.61	0.989	0.978	1
598	extrapolated	1	7.592	6.559	8.625	0.99	0.978	1.001
621	extrapolated	1	7.605	6.57	8.639	0.99	0.979	1.001
644	extrapolated	1	7.617	6.58	8.653	0.991	0.98	1.002
667	extrapolated	1	7.628	6.59	8.666	0.992	0.981	1.003
690	extrapolated	1	7.639	6.599	8.678	0.992	0.981	1.003
713	extrapolated	1	7.649	6.608	8.69	0.993	0.982	1.004
736	extrapolated	1	7.659	6.616	8.701	0.993	0.983	1.004
759	extrapolated	1	7.668	6.624	8.712	0.994	0.983	1.005
782	extrapolated	1	7.676	6.631	8.722	0.994	0.984	1.005
805	extrapolated	1	7.685	6.638	8.731	0.995	0.985	1.005
828	extrapolated	1	7.693	6.645	8.74	0.995	0.985	1.005
851	extrapolated	1	7.7	6.652	8.748	0.996	0.986	1.006
874	extrapolated	1	7.707	6.658	8.756	0.996	0.986	1.006
1	interpolated	2	1	1	1	0.275	0.234	0.317
25	interpolated	2	3.285	2.845	3.726	0.808	0.778	0.838
49	interpolated	2	3.446	2.949	3.942	0.865	0.846	0.883
73	interpolated	2	3.505	2.987	4.022	0.892	0.878	0.905
97	interpolated	2	3.535	3.006	4.064	0.91	0.899	0.921
121	interpolated	2	3.554	3.018	4.089	0.923	0.913	0.933
146	interpolated	2	3.567	3.026	4.107	0.934	0.925	0.943
170	interpolated	2	3.576	3.031	4.12	0.942	0.933	0.951
194	interpolated	2	3.582	3.036	4.129	0.948	0.939	0.957
218	interpolated	2	3.588	3.039	4.136	0.954	0.945	0.963

m	method	order	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
242	interpolated	2	3.592	3.042	4.142	0.959	0.949	0.968
266	interpolated	2	3.595	3.044	4.147	0.963	0.953	0.972
291	interpolated	2	3.598	3.046	4.151	0.967	0.957	0.976
315	interpolated	2	3.601	3.047	4.154	0.97	0.96	0.98
339	interpolated	2	3.603	3.048	4.157	0.973	0.963	0.983
363	interpolated	2	3.605	3.05	4.16	0.976	0.966	0.986
387	interpolated	2	3.606	3.051	4.162	0.978	0.968	0.988
411	interpolated	2	3.608	3.051	4.164	0.98	0.969	0.99
436	interpolated	2	3.609	3.052	4.166	0.982	0.971	0.992
437	observed	2	3.609	3.052	4.166	0.982	0.971	0.992
438	extrapolated	2	3.609	3.052	4.166	0.982	0.971	0.992
460	extrapolated	2	3.61	3.053	4.167	0.983	0.972	0.994
483	extrapolated	2	3.611	3.054	4.169	0.984	0.974	0.995
506	extrapolated	2	3.612	3.054	4.17	0.986	0.975	0.996
529	extrapolated	2	3.613	3.055	4.171	0.987	0.976	0.998
552	extrapolated	2	3.614	3.055	4.172	0.988	0.977	0.998
575	extrapolated	2	3.614	3.056	4.173	0.989	0.978	0.999
598	extrapolated	2	3.615	3.056	4.174	0.99	0.979	1
621	extrapolated	2	3.616	3.056	4.175	0.99	0.98	1.001
644	extrapolated	2	3.616	3.057	4.176	0.991	0.981	1.001
667	extrapolated	2	3.617	3.057	4.176	0.992	0.982	1.002
690	extrapolated	2	3.617	3.057	4.177	0.992	0.983	1.002
713	extrapolated	2	3.617	3.057	4.178	0.993	0.983	1.002
736	extrapolated	2	3.618	3.058	4.178	0.993	0.984	1.003
759	extrapolated	2	3.618	3.058	4.179	0.994	0.985	1.003
782	extrapolated	2	3.619	3.058	4.179	0.994	0.986	1.003
805	extrapolated	2	3.619	3.058	4.18	0.995	0.986	1.003
828	extrapolated	2	3.619	3.059	4.18	0.995	0.987	1.003
851	extrapolated	2	3.62	3.059	4.18	0.996	0.988	1.004
874	extrapolated	2	3.62	3.059	4.181	0.996	0.988	1.004

Table S7: USPC-1014 Hill number (q = 0, 1, 2) data for pollen count. m = sample size for the diversity estimates of order q are computed; method states whether the estimate has been interpolated, extrapolated, or observed and depends on if m is less than, equal to, or greater than the sample size; order relates to the diversity order selected (q = 0, 1, 2); qD is equal to the estimate diversity of order q for the sample size of m; SC is equal to the estimated sample coverage for the sample size of m; qD.LCL & qD.UCL equal the bootstrapped lower and upper confidence limits (0.95) for the diversity order q; SC.LCL & SC.UCL equal the bootstrapped lower and upper confidence limits (0.95) for the predicted sample coverage (Hsieh et al. 2016).

m	method	order	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
1	interpolated	0	1	1	1	0.384	0.339	0.428
24	interpolated	0	6.631	6.012	7.249	0.852	0.83	0.875
48	interpolated	0	9.54	8.507	10.573	0.9	0.882	0.918
72	interpolated	0	11.674	10.308	13.04	0.921	0.906	0.936
96	interpolated	0	13.411	11.765	15.057	0.934	0.92	0.947
120	interpolated	0	14.894	13.003	16.785	0.943	0.93	0.955
144	interpolated	0	16.187	14.075	18.3	0.95	0.938	0.961
167	interpolated	0	17.286	14.976	19.595	0.955	0.944	0.966
191	interpolated	0	18.31	15.806	20.814	0.96	0.949	0.97
215	interpolated	0	19.232	16.543	21.921	0.964	0.953	0.974
239	interpolated	0	20.068	17.201	22.936	0.967	0.956	0.977
263	interpolated	0	20.834	17.793	23.875	0.969	0.959	0.98
287	interpolated	0	21.541	18.33	24.753	0.972	0.961	0.982
310	interpolated	0	22.173	18.8	25.547	0.973	0.963	0.984
334	interpolated	0	22.793	19.253	26.333	0.975	0.965	0.985
358	interpolated	0	23.379	19.673	27.084	0.976	0.966	0.986
382	interpolated	0	23.935	20.066	27.805	0.977	0.967	0.988
406	interpolated	0	24.468	20.435	28.501	0.978	0.968	0.989
430	interpolated	0	24.979	20.784	29.174	0.979	0.969	0.99
431	observed	0	25	20.798	29.202	0.979	0.969	0.99
432	extrapolated	0	25.021	20.812	29.23	0.979	0.969	0.99
454	extrapolated	0	25.471	21.115	29.828	0.98	0.969	0.99
477	extrapolated	0	25.926	21.415	30.438	0.981	0.97	0.991
499	extrapolated	0	26.347	21.686	31.007	0.981	0.971	0.992
522	extrapolated	0	26.771	21.953	31.588	0.982	0.971	0.993
545	extrapolated	0	27.18	22.204	32.157	0.983	0.972	0.993
567	extrapolated	0	27.559	22.429	32.688	0.983	0.972	0.994
590	extrapolated	0	27.941	22.649	33.232	0.984	0.973	0.995
613	extrapolated	0	28.309	22.853	33.765	0.984	0.973	0.995
635	extrapolated	0	28.65	23.035	34.265	0.985	0.974	0.996
658	extrapolated	0	28.993	23.21	34.776	0.985	0.974	0.996
680	extrapolated	0	29.311	23.366	35.255	0.986	0.975	0.997
703	extrapolated	0	29.631	23.516	35.747	0.986	0.975	0.997
726	extrapolated	0	29.941	23.654	36.228	0.987	0.976	0.998
748	extrapolated	0	30.226	23.774	36.678	0.987	0.977	0.998
771	extrapolated	0	30.515	23.89	37.14	0.988	0.977	0.998
794	extrapolated	0	30.793	23.995	37.592	0.988	0.978	0.999
816	extrapolated	0	31.051	24.086	38.015	0.989	0.978	0.999
839	extrapolated	0	31.31	24.172	38.448	0.989	0.979	0.999
862	extrapolated	0	31.561	24.25	38.872	0.989	0.979	1
1	interpolated	1	1	1	1	0.384	0.334	0.434
24	interpolated	1	3.603	3.144	4.062	0.852	0.826	0.878
48	interpolated	1	4.063	3.486	4.639	0.9	0.88	0.92
72	interpolated	1	4.286	3.649	4.923	0.921	0.905	0.938
96	interpolated	1	4.424	3.75	5.099	0.934	0.919	0.948

m	method	order	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
120	interpolated	1	4.52	3.819	5.222	0.943	0.929	0.956
144	interpolated	1	4.592	3.871	5.313	0.95	0.936	0.963
167	interpolated	1	4.645	3.909	5.381	0.955	0.942	0.968
191	interpolated	1	4.69	3.941	5.439	0.96	0.947	0.972
215	interpolated	1	4.727	3.968	5.486	0.964	0.951	0.976
239	interpolated	1	4.758	3.99	5.526	0.967	0.955	0.979
263	interpolated	1	4.784	4.009	5.56	0.969	0.958	0.981
287	interpolated	1	4.807	4.025	5.589	0.972	0.96	0.983
310	interpolated	1	4.826	4.038	5.613	0.973	0.962	0.985
334	interpolated	1	4.843	4.05	5.636	0.975	0.964	0.986
358	interpolated	1	4.859	4.061	5.656	0.976	0.965	0.988
382	interpolated	1	4.873	4.071	5.674	0.977	0.966	0.989
406	interpolated	1	4.885	4.08	5.691	0.978	0.967	0.99
430	interpolated	1	4.897	4.088	5.706	0.979	0.968	0.991
431	observed	1	4.897	4.089	5.706	0.979	0.968	0.991
432	extrapolated	1	4.898	4.089	5.707	0.979	0.968	0.991
454	extrapolated	1	4.908	4.096	5.719	0.98	0.968	0.991
477	extrapolated	1	4.917	4.103	5.732	0.981	0.969	0.992
499	extrapolated	1	4.926	4.109	5.744	0.981	0.97	0.993
522	extrapolated	1	4.935	4.115	5.755	0.982	0.97	0.994
545	extrapolated	1	4.944	4.121	5.767	0.983	0.971	0.994
567	extrapolated	1	4.952	4.127	5.777	0.983	0.971	0.995
590	extrapolated	1	4.959	4.132	5.787	0.984	0.972	0.996
613	extrapolated	1	4.967	4.137	5.797	0.984	0.972	0.996
635	extrapolated	1	4.974	4.142	5.806	0.985	0.973	0.997
658	extrapolated	1	4.981	4.147	5.814	0.985	0.973	0.997
680	extrapolated	1	4.987	4.151	5.823	0.986	0.974	0.998
703	extrapolated	1	4.993	4.156	5.831	0.986	0.975	0.998
726	extrapolated	1	4.999	4.16	5.839	0.987	0.975	0.999
748	extrapolated	1	5.005	4.164	5.846	0.987	0.976	0.999
771	extrapolated	1	5.01	4.167	5.853	0.988	0.976	0.999
794	extrapolated	1	5.015	4.171	5.86	0.988	0.977	1
816	extrapolated	1	5.02	4.174	5.866	0.989	0.977	1
839	extrapolated	1	5.025	4.178	5.872	0.989	0.978	1
862	extrapolated	1	5.03	4.181	5.878	0.989	0.978	1
1	interpolated	2	1	1	1	0.384	0.332	0.436
24	interpolated	2	2.442	2.149	2.736	0.852	0.832	0.872
48	interpolated	2	2.521	2.202	2.841	0.9	0.883	0.917
72	interpolated	2	2.549	2.22	2.878	0.921	0.906	0.936
96	interpolated	2	2.563	2.229	2.896	0.934	0.92	0.948
120	interpolated	2	2.571	2.235	2.908	0.943	0.929	0.956
144	interpolated	2	2.577	2.238	2.916	0.95	0.936	0.963
167	interpolated	2	2.581	2.241	2.921	0.955	0.942	0.968
191	interpolated	2	2.584	2.243	2.925	0.96	0.947	0.972
215	interpolated	2	2.586	2.244	2.928	0.964	0.951	0.976

m	method	order	qD	qD.LCL	qD.UCL	SC	SC.LCL	SC.UCL
239	interpolated	2	2.588	2.246	2.931	0.967	0.955	0.979
263	interpolated	2	2.59	2.247	2.933	0.969	0.958	0.981
287	interpolated	2	2.591	2.248	2.935	0.972	0.961	0.983
310	interpolated	2	2.592	2.248	2.936	0.973	0.963	0.984
334	interpolated	2	2.593	2.249	2.937	0.975	0.964	0.986
358	interpolated	2	2.594	2.249	2.939	0.976	0.966	0.987
382	interpolated	2	2.595	2.25	2.94	0.977	0.967	0.988
406	interpolated	2	2.595	2.25	2.94	0.978	0.968	0.989
430	interpolated	2	2.596	2.251	2.941	0.979	0.968	0.99
431	observed	2	2.596	2.251	2.941	0.979	0.968	0.99
432	extrapolated	2	2.596	2.251	2.941	0.979	0.968	0.99
454	extrapolated	2	2.596	2.251	2.942	0.98	0.969	0.991
477	extrapolated	2	2.597	2.251	2.942	0.981	0.97	0.991
499	extrapolated	2	2.597	2.252	2.943	0.981	0.97	0.992
522	extrapolated	2	2.598	2.252	2.943	0.982	0.971	0.993
545	extrapolated	2	2.598	2.252	2.944	0.983	0.971	0.994
567	extrapolated	2	2.598	2.252	2.944	0.983	0.972	0.994
590	extrapolated	2	2.599	2.252	2.945	0.984	0.973	0.995
613	extrapolated	2	2.599	2.253	2.945	0.984	0.973	0.995
635	extrapolated	2	2.599	2.253	2.945	0.985	0.974	0.996
658	extrapolated	2	2.599	2.253	2.946	0.985	0.974	0.996
680	extrapolated	2	2.6	2.253	2.946	0.986	0.975	0.997
703	extrapolated	2	2.6	2.253	2.946	0.986	0.976	0.997
726	extrapolated	2	2.6	2.253	2.947	0.987	0.976	0.998
748	extrapolated	2	2.6	2.253	2.947	0.987	0.977	0.998
771	extrapolated	2	2.6	2.254	2.947	0.988	0.977	0.998
794	extrapolated	2	2.6	2.254	2.947	0.988	0.978	0.999
816	extrapolated	2	2.601	2.254	2.947	0.989	0.978	0.999
839	extrapolated	2	2.601	2.254	2.948	0.989	0.979	0.999
862	extrapolated	2	2.601	2.254	2.948	0.989	0.979	0.999

Table S8: C-626937 Hill number (q = 0, 1, 2) data for pollen count. m = sample size for the diversity estimates of order q are computed; method states whether the estimate has been interpolated, extrapolated, or observed and depends on if m is less than, equal to, or greater than the sample size; order relates to the diversity order selected (q = 0, 1, 2); qD is equal to the estimate diversity of order q for the sample size of m; SC is equal to the estimated sample coverage for the sample size of m; qD.LCL & qD.UCL equal the bootstrapped lower and upper confidence limits (0.95) for the diversity order q; SC.LCL & SC.UCL equal the bootstrapped lower and upper confidence limits (0.95) for the predicted sample coverage (Hsieh et al. 2016).

Locality	n (dicots only)	Simpson's Diversity (1-D)	Shannon index (H)	Shannon Evenness (EH)
USPC-1014	207	0.551	1.131	0.212
USPC-1005	317	0.494	1.138	0.198
Harvard Forest (Pooled)	931	0.815	1.843	0.270
Harvard Forest (Bag #5)	377	0.658	1.308	0.221

Table S9: Results from modern ecological diversity metrics used to assess diversity of the fossil macroflora sites USPC-1014, USPC-1005 compared against a modern forest sample (pooled), and a single bag from the Harvard Forest modern flora sample (*1*). Fossil megaflora localities are similar in regards to richness and evenness. The pooled Harvard Forest sample is more diverse than the fossil localities, however, this may be a function of sample size—this is evidenced from a run using only a single bag from the Harvard Forest, which produced similar diversity measurements to the fossil megaflora localities.

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